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BIRDS OF THE ST. CROIX RIVER VALLEY: MINNESOTA AND WISCONSIN

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Library of Congress Cataloging in Publication Data

Faanes, Craig A.
Birds of the St. Croix River Valley, Minnesota and Wisconsin.

(North American fauna ; no. 73)
Includes bibliographical references and index.
Supt. of Docs. no.: I 49.30:73
1. Birds—Saint Croix Valley (Wis. and Minn.). I. Title. II. Series.
QL155.A4 no. 73 [QL683.S23] 596.097s 81-607022
[598.29775'1] AACR2

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BIRDS OF THE ST. CROIX RIVER VALLEY: MINNESOTA AND WISCONSIN

by

Craig A. Faanes

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
North American Fauna, Number 73

Washington, D.C. • 1981

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Dedicated to
Samuel D. Robbins, Jr.
Ornithologist and Friend

Birds of the St. Croix River Valley: Minnesota and Wisconsin

by

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Abstract

The St. Croix River Valley encompasses nearly 11,550 km^2 in east-central Minnesota and northwestern Wisconsin. A wide range of habitats are available for birds including upland oak, lowland deciduous, maple-basswood, lowland and upland coniferous forests, natural basin wetlands, and grasslands. Situated in the north-central region of the United States, the valley is a biological "crossroads" for many species. Because of the mixed affinities of plant communities, the valley includes the northern and southern range limits for a number of species. Also, because the valley lies near the forest-prairie transition zone, many typical western breeding species (e.g. pintail, western meadowlark, yellow-headed blackbird) breed in proximity to typical eastern species such as tufted titmouse, eastern meadowlark, and cardinal.

From 1966 to 1980, I conducted extensive surveys of avian distribution and abundance in the St. Croix River Valley. I have supplemented the results of these surveys with published and unpublished observations contributed by many ornithologists. These additional data include compilations from Christmas Bird Counts sponsored by the National Audubon Society and from the Breeding Bird Survey coordinated by the U.S. Fish and Wildlife Service. Three hundred fourteen species have been recorded in the study area; data are presented on the migration period, nesting season distribution, winter distribution, relative abundance, and habitat use of each species.

Recognizing the uniqueness of the area, and its importance not only to wildlife but also to man, the U.S. Congress designated the St. Croix a National Scenic Riverway. This action provided a considerable degree of protection to lands along and directly adjacent to the river. Unfortunately, no similar legal measure exists to protect lands away from the river. With the exception of the northern quarter of the St. Croix River Valley, agricultural interests have made significant inroads into the habitat base. The continuing expansion of the nearby Minneapolis-St. Paul metropolitan region has degraded or destroyed many woodlots, upland fields, and wetlands. In numerous instances, degradation of natural habitats has influenced the abundance and distribution of bird species. Because of these changes, both the Federal government and State Departments of Natural Resources have listed several species in various categories based on their current status. In the St. Croix River Valley, seven species are endangered, eight are threatened, and 29 are watch or priority status in either or both states. Data presented in this report are of value to land managers, land use specialists, and ornithologists, in assessing current and projected habitat alterations on the avifauna of this valley.

The St. Croix River bisects a large region of western Wisconsin and east central Minnesota that exhibits a wide range of habitat types. This region supports not only birds, but many mammals, fishes, reptiles and amphibians, and several thousand species of vascular and nonvascular plants. The river itself is relatively clean through most of its course, and its natural flow is interrupted by only two small dams.

Because the river lies within a 1-day drive of nearly 10 million people (Waters 1977), use of the area for recreational purposes is extremely heavy. Recreational pursuits include sunbathing, boating, and wild river kayaking in the summer, and ice fishing and cross-country skiing in the winter. The large number of unique and highly fragile habitats that exist there may never be compatible with the uses and abuses of the land that go with expanding human populations.

Through the efforts of a number of citizens concerned with the quality of their environment and the foresightedness of several local, State, and Federal legislators, a portion of the upper St. Croix River Valley (hereafter termed "the Valley") was established as a National Wild and Scenic River. Through establishment of the National Wild and Scenic Rivers Act (P.L. 90:542), the ground rules were established to preserve free-flowing streams that have "outstandingly remarkable scenic, recreational, geologic, fish and wildlife, historic, cultural, and other similar values." Any person who has spent time along a stretch of the St. Croix would have to agree that this river meets or exceeds all the criteria that the Act established.

The history of this magnificent valley is cloaked with the adventures of lumber barons, trappers and hunters, commercial fishermen, and many others. During the days of the early voyageurs, the river served as a vital link between the Great Lakes and the growing Minneapolis–St. Paul area. Excellent descriptions of the colorful history of the Valley are provided by Link (1977) and Waters (1977).

Although the Scenic River Act provides considerable protection for the lands and resources directly adjacent to the river, there is no comparable legal measure to protect lands not bordering the river. Several man-influenced impacts are escalating in the Valley and provide a continual threat to remaining resources. Two influences providing the greatest threat to the natural resources of the Valley are urban expansion and agricultural production. First, the continual, almost unabated spread of urban development has already had a profound impact on existing habitats. Second, agriculture has had a growing impact on bird life in the Valley. Lands producing row crops, small grains, and hay in St. Croix County in 1967 totaled 75,910 ha. This acreage increased 17.4% to 88,057 ha by 1977 (U.S. Department of Agriculture, personal communication). The total hectarage of lands in agricultural production (row crops and hay) made up 16 and 18.8% of the Valley in 1967 and 1977, respectively. These examples suggest the magnitude of the impact that agriculture has had upon wildlife resources in the past two decades.

It can be argued that the agricultural hectarages cited above represent changes in cropping practices rather than actual increases in the hectarage of wildlife habitat converted to agricultural production. However, increased technology and the growth of agribusiness have resulted in a shift to fencerow to fencerow farming with serious impacts on many upland habitats.

Wetland habitats have also been significantly reduced. Peterson (1978) showed that over 27% of the seasonal wetlands (Type III of Shaw and Fredine 1956) in St. Croix County were drained between 1958 and 1977.

The objective of this report is to provide, in condensed form, an account of the 314 bird species that have been recorded in the Valley.

Climate

The Valley has a temperate, continental climate that is characterized by extreme seasonal variability. Mean monthly air temperatures are -12 to -9°C in January and 20 to 22°C in July. The average growing season ranges from 100 days in the north (Burnett and Pine counties) to over 120 days in the south (St. Croix and Washington counties). The ground is frozen usually from late November through mid-April and frost depths range from 66 to 86 cm.

Mean annual precipitation is 74.4 cm (Young and Hindall 1973). The range in yearly precipitation is about 71.1 cm at St. Croix Beach, Washington County, to nearly 78.7 cm at Grantsburg, Burnett County (Lindholm et al. 1974). Periods of prolonged drought are highly infrequent. February is usually the driest month (< 2.5 cm) and June the wettest (12.2 cm). Annual evapotranspiration from the St. Croix watershed is 59.4 cm (Lindholm et al. 1974). During July and August, when temperatures are highest and plant moisture demands are greatest, evapotranspiration often exceeds precipitation.

Geology

Interpretations of the interrelation of birds and other wildlife with their environment require an understanding of the geology and soils of an area. The St. Croix River Valley is an area rich in geologic history. Sediments and rock formations throughout the Valley range in geologic age from the 1-billion-year-old Precambrian lava flows at Interstate Park to very recent sediment deposition at the mouth of the Kinnickinnic River.

Bedrock in the upper portion of the Valley consists primarily of Precambrian igneous lava flows, shales, sandstones, and igneous and metamorphic crystalline formations. Bedrock of the lower portions of the Valley consists of marine sandstones, shales, and limestones that were deposited during the Cambrian and Ordovician periods. Outcroppings southward through the Valley indicate that bedrock formations are progressively younger.

Glacial deposits consist mainly of undifferentiated till that was deposited as the last glacier melted about 10,000 years ago. This glacial action was very important in forming the current features of the landscape. Especially important and characteristic among these glacial deposits are the extensive sandy soils associated with the bed of Glacial Lake Grantsburg in Burnett and Pine counties, and the numerous prairie pothole-type wetlands that occur in Polk, St. Croix, and Washington counties.

One important result of past glacial activity in the St. Croix River Valley is the highly productive soils that formed on the glacial outwash. Through the combined action of climate, vegetation, and proper acidity of these glacial deposits, soils developed that are very important for agricultural production. Productivity of all soils in the Valley is, of course, not equal. Soil conditions range from the sandy, acidic beach-derived soils associated with Glacial Lake Grantsburg, to the deep, rich loams and silt loam prairie soils of the lower Valley. Productivity of these soils for wildlife appears to correlate nicely. For example, the acidic soils of Glacial Lake Grantsburg are usually associated with relatively sterile Jack Pine Barren forest which supports limited wildlife populations. On the other extreme, the deep, rich prairie soils of the southern regions produce exceptional agricultural crops and also support large and highly diverse wildlife populations.

Physiography and Land Use

The diverse physiographic and topographic features of the Valley result from at least four different glacial epochs that extended from 1 million to 10,000 years ago. The St. Croix River itself is an important component of past and present physiographic changes. The gradient of the river averages 102 cm per km across its entire course, ranging from nearly zero on Lake St. Croix to 4.3 m per km at the Kettle River Rapids, Pine County (Young and Hindall 1973). Altitude of the land surface ranges from about 207 m above sea level at Prescott to about 518 m near Cable at the upper end of the Namekagon River. The interior of the Valley has a general slope ranging from 427 m in the north to about 305 m in the south.

During the last glacial period the St. Croix served as a major drainage for glacial melt waters. Martin (1932) reported that the post-glacial course of the river contained the Apple River Valley in western Wisconsin. In preglacial times, the major course of the river was farther west in Minnesota. In addition to carrying melt waters from the glacier, the St. Croix carried overflow waters from large glacial lakes that occurred in the Lake Superior basin. One outlet was the valley at Solon Springs which is now occupied by St. Croix Lake, the headwaters of the river (Young and Hindall 1973).

Topography of the Valley includes flat-topped, steep-sided sedimentary hills adjacent to the river, and narrow stream valleys in the extreme lower reaches. The remainder of the Valley is composed primarily of broad, flat glacial outwash plains and kettle and knob topography associated with terminal and end moraines.

Lakes and marshes are abundant in the northern half of the Valley where surface drainage systems are poorly developed. One unique drainage system in southern Pine County is separated from all other watersheds in the region by a zone of elevated igneous bedrock. Marshes and streams in this region are characterized by low alkalinity and a deep brownish stained color (Waters 1977). In the southern reaches of the Valley, alkalinity and vegetation of lakes and marshes become progressively greater owing primarily to limestone and sandstone bedrock.

The entire St. Croix watershed encompasses about 11,550 km² (1.7 million ha). The river drains about 7,233 km² in Wisconsin and 4,317 km² in Minnesota (Lindholm et al. 1974). Included in the watershed are all or part of

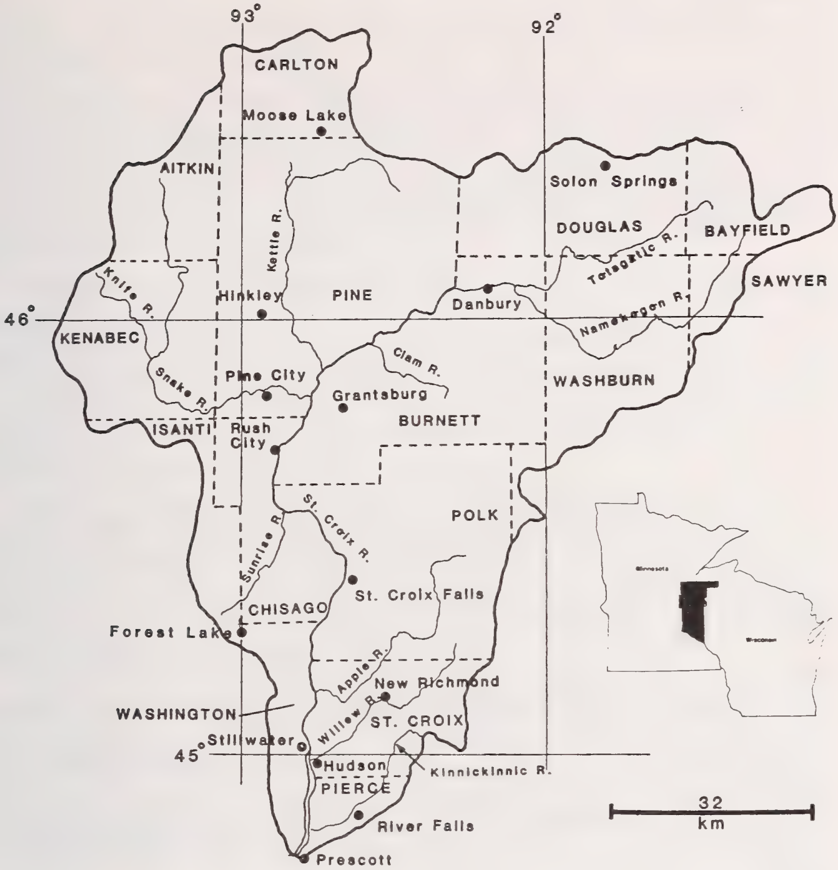

Fig. 1. The St. Croix River watershed, including Minnesota and Wisconsin, encompasses nearly 11,550 km².

18 counties, 9 in each State (Fig. 1). There are eight major streams or watersheds that are tributary to the St. Croix, including the Snake and Kettle rivers, and Pine County streams in Minnesota (Waters 1977), and the Namekagon, Clam, Apple, Willow, and Kinnickinnic rivers in Wisconsin.

Related to the tremendous amount of diversity and variability in the topography and geology of the St. Croix River Valley, various geographers and plant ecologists have developed systems for classifying landforms and major vegetative communities (Fig. 2). These systems have provided divisions that are important in understanding the interrelation of bird distribution with vegetation and geomorphic features. Two separate systems have been developed, one for each State. Both systems have considerable merit considering the foundation upon which they were based. Unfortunately, these separate systems make interpretation of bird distribution awkward when considering the two States. Following is a brief overview of these

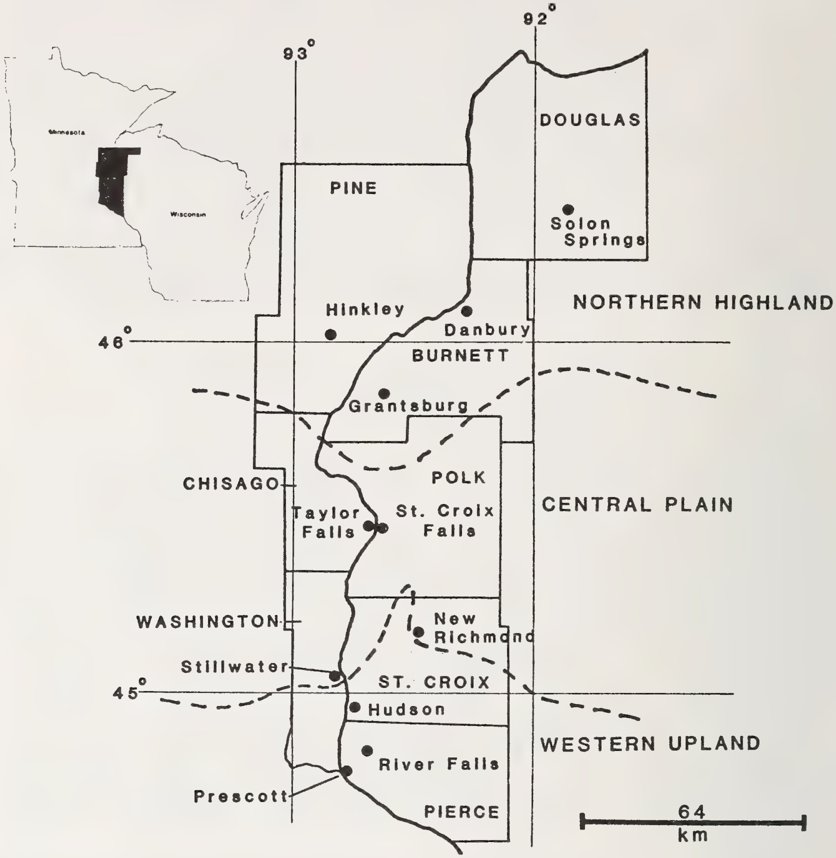

Fig. 2. Major physiographic regions of the St. Croix River Valley.

major divisions by State and the reasons for the combining of systems that I had to consider for interpretation.

The most usable division system for Minnesota was developed by Kratz and Jensen (1977). They developed a system based on both major vegetational and geomorphic provinces and included 17 distinct Ecological–Geomorphic divisions. Four of these divisions are included in the Minnesota counties. A brief description of each follows.

Southern Oak Barrens Section.—This section includes a large region of southeastern Minnesota generally referred to as the Driftless Area, which was not covered by ice during glacial periods. In the Valley, about 80% of Washington County is included in this section. Topography is characterized by highly dissected limestone and sandstone hills adjacent to the St. Croix River. Away from the river, large expanses of glacial outwash and kettle and knob topography predominate. Vegetation consists of a transition between prairie and deciduous forests. Originally, oak barrens and savannah occurred throughout this area.

Mississippi River Sand Plains Section.—This section includes a small portion of northwestern Washington and southwestern Chisago counties where topography is characteristic of glacial outwash plains—including broad, flat areas with occasional wetland basins interspersed. Original vegetation of the sand outwash soils was primarily oak forest with scattered prairie openings and wet prairie in depressions.

Grantsburg Section.—This section includes most of Chisago County and a small part of southern Pine County. Topography is characterized by flat to gently rolling glacial sediments that are frequently dissected by streams. The Grantsburg section includes the bed of Glacial Lake Grantsburg, which extended eastward into Burnett County, Wisconsin. Vegetation originally included Jack Pine Barrens and scattered oak openings. Currently, much of the land is in agricultural production.

Mille Lacs Section.—This section includes most of southern and all of northern Pine County. Topography is characterized by glacial scoured bedrock and glacial till that provide a kettle and knob topography. Forest-bordered lakes are numerous throughout this section. Vegetation is characterized by mixed northern hardwood and coniferous stands with conifer bogs interspersed throughout.

The classification system used in Wisconsin (Martin 1932) is based primarily on physiographic features and bedrock geology, regardless of vegetation. However, the influence of physiography on vegetation is well demonstrated in Wisconsin because the regions that occur in the Valley each support entirely different vegetative communities. Martin considered five distinct physiographic provinces in Wisconsin and the Valley is included in three.

Western Upland.—This region in the Valley is the northern extension of the Driftless Area, a part of Wisconsin, Minnesota, and Illinois that was not covered by glacial ice. Included in the Western Upland are the highly dissected stream valleys adjacent to the St. Croix River and the broad and gently rolling glacial outwash plain of central St. Croix County. Original vegetation included Southern Oak Forest in the dissected area and Tall Grass Prairie associated with the outwash plain. At present, much of the Western Upland is in agricultural production. Portions of central St. Croix, southern Polk, and central Washington counties are dotted with numerous natural basin wetlands.

Central Plain.—This region includes northern St. Croix, southern Burnett, and most of Polk counties. Topography of the Central Plain is also characterized by broad glacial outwash plains lying over Cambrian sandstone in the southern regions. Extensive areas of kettle and knob topography associated with end moraines occur in the north. Numerous lakes and bogs are associated with this topography. Vegetation consists of a mixture of southern oak forest, prairie and northern mixed hardwood, and coniferous forest.

Northern Highland.—This region, which includes northern Burnett and southern Douglas counties, has topography characteristic of morainal deposits and includes numerous high, rounded hills composed of more resistant bedrock. Geology of this region is primarily highly resistant Precambrian igneous rock, quite unlike southern regions of the Valley. Original vegetation of the Northern Highland was composed almost exclusively of pine forest and coniferous bogs. Presently, the pine forest exists only as scattered remnants interspersed throughout extensive mixed second growth deciduous and coniferous forest. Large lakes and extensive bogs are characteristic of the Northern Highland.

This brief discussion of the major physiographic regions of the St. Croix River Valley points out both similarities and differences between the systems developed for each State. For the sake of convenience and clarity in describing bird occurrence and distribution, I have combined both systems. Thus, throughout this report reference to the Western Upland will include the Wisconsin areas outlined in Martin (1932) and the Southern Oak Barrens region of Minnesota described by Kratz and Jensen (1977). The Central Plain will include the Wisconsin areas outlined and those areas of Chisago and Washington counties included in the Mississippi River Sand Plains and the Grantsburg Section. Reference to the Northern Highland will include the Wisconsin areas and the Mille Lacs Section in Pine County. These agree closely with the physiographic regions used by the U.S. Fish and Wildlife Service's Breeding Bird Survey (BBS; Bystrak 1979).

Habitats and Bird Distribution

Within the Valley, a wide range of vegetational communities are available to birds: deciduous and coniferous forest, wetlands, agricultural lands, and urban–residential areas. Original vegetation of the Valley as described by Curtis (1959) and Marschner (1930) included Tall Grass Prairie and Oak Savannah in the Western Upland, Southern Hardwood Forest (primarily oak) and Tall Grass Prairie in the Central Plain, and mixed Coniferous–Deciduous Forest association in the Northern Highland (Fig. 3). Much of the bed of Glacial Lake Grantsburg was composed of relatively sterile jack pine and oak forest. (Scientific names of plants are given in Appendix A.)

Man's presence has had a profound impact on the composition, distribution, and extent of these major communities. The Tall Grass Prairie which may have lapped at the shoulders of early settlers is now field and pastures. The prairie is now confined to railroad rights-of-way and small odd corners that would not accommodate a plow. The majestic white pine forest that once blanketed most of the northern regions has been reduced to scattered remnants.

Habitat changes that adversely affect some bird species often encourage expansion of other species. The clearing of forests of northern white pine has allowed a second growth deciduous disclimax habitat type to develop. Land clearing for agriculture was very important to the advance of the greater prairie chicken (scientific names of birds are given in the species accounts) in this region. Early accounts make vivid reference to the large number of greater prairie chickens that occurred after moderate agricultural expansion. However, the rapacious clearing that accompanied intensified agricul-

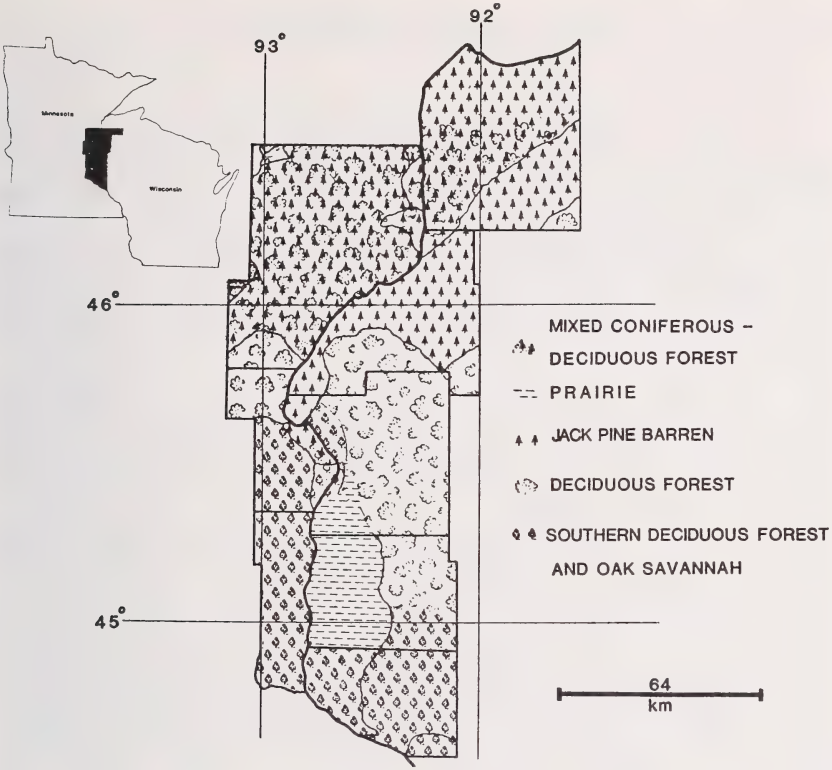
92°
93°
Minnesota
Wisconsin
46°
45°
MIXED CONIFEROUS – DECIDUOUS FOREST
PRAIRIE
JACK PINE BARREN
DECIDUOUS FOREST
SOUTHERN DECIDUOUS FOREST AND OAK SAVANNAH
64 km

Fig. 3. Major vegetative communities of the St. Croix River Valley, adapted from Curtis (1959) and Marschner (1930).

tural production also caused the demise of the greater prairie chicken as a natural breeding bird.

An important environmental characteristic that affects bird occurrence and distribution is described by Curtis (1959) as the "Tension Zone." Based on a combination of environmental factors including soil type, annual precipitation, temperature, and geology, this zone of vegetational range extremes has a profound effect on the distribution of many bird species in the Valley. Essentially, this zone is the north–south limit area for many boreal forest and oak forest forbs, shrubs and trees. This contact zone was shown by Beimborn (1969) as important to the distribution of at least 14 bird species in Wisconsin. Robbins (1974*b*) demonstrated the influence of the Tension Zone on the breeding range limits of the alder and willow flycatchers.

Nineteen distinct habitat categories have been identified. Each is presented here in terms of size, distribution, floral characteristics, and characteristic breeding birds. Breeding bird species that apparently reach their greatest density in a specific habitat are marked with an asterisk. Habitat use by migrants will be considered individually with each species account.

Deciduous Forest Communities

Northern Hardwood Forest

This floristic community extends throughout the Northern Highland and much of the Central Plain north of St. Croix Falls (Polk and Chisago counties). Characterized by a mixture of coniferous and deciduous tree types, the Northern Hardwood Forest occurs on a wide range of topographic sites and on many soil types. Mesic sites support white birch, sugar maple, hemlock, basswood, and red oak. Important coniferous species of this habitat are red pine, white pine, and to a limited extent jack pine. Depending on the extent of early successional stages this is generally a climax or near-climax community.

Prevalent within the shrub layer and among ground layer species are beaked hazel, bracken fern, wood anemone, wild sarsaparilla, big-leaf aster, blue bead lily, northern bedstraw, ground pine, Canada mayflower, bishop's cap, Solomon's seal, twisted stalk, starflower, downy yellow violet, rice grass, and Pennsylvania sedge.

Characteristic breeding birds include broad-winged Hawk*, ruffed grouse*, great horned owl, barred owl, black-billed cuckoo*, common flicker, yellow-bellied sapsucker*, hairy woodpecker*, downy woodpecker, great crested flycatcher, least flycatcher*, eastern wood pewee*, blue jay, northern raven, black-capped chickadee, white-breasted nuthatch, American robin, wood thrush, veery*, solitary vireo, red-eyed vireo*, black-and-white warbler, chestnut-sided warbler, ovenbird*, American redstart, northern oriole, scarlet tanager, rose-breasted grosbeak*, and white-throated sparrow.

Lowland Deciduous Forest

This rich deciduous community occurs primarily along the floodplains of larger streams and rivers adjacent to the St. Croix in the Western Upland and Central Plain. The abundant soil moisture from river flooding and high water table is a principal microclimatic feature of this community. Because of its southern plant affinity, Lowland Deciduous Forest attracts some typically southern breeding bird species that occur in no other habitat type. Major tree species characteristic of this community are silver maple, American elm, green ash, red oak, basswood, and cottonwood.

Prevalent species in the shrub layer are black willow, box-elder, and gray dogwood. Depending on the amount of disturbance by grazing cattle, tartarian honeysuckle and prickly ash approach dominance in the shrub layer. Important among ground layer species are jack-in-the-pulpit, toothwort, Virginia waterleaf, wood nettle, poison ivy, germander, hedge nettle, jewelweed, and skunk cabbage.

Characteristic breeding bird species of the Lowland Deciduous Forest include great blue heron*, wood duck*, red-shouldered hawk*, yellow-billed cuckoo, screech owl*, barred owl*, pileated woodpecker*, red-bellied woodpecker*, downy woodpecker, eastern wood pewee, tufted titmouse*, white-breasted nuthatch*, blue-gray gnatcatcher*, yellow-throated vireo*, warbling vireo*, blue-winged warbler*, yellow warbler, cerulean warbler*, Louisiana waterthrush*, northern oriole*, scarlet tanager*, and rose-breasted grosbeak.

Southern Deciduous Forest

This habitat type includes a closed-canopy upland community that is generally restricted to the region south of the Tension Zone in the Western Upland and Central Plain. Southern Deciduous Forest occurs almost exclusively on dry, well-drained upland sites. Before settlement of this region, Southern Deciduous Forest existed as part of an oak forest intermixed with prairie giving the area aspects of a savannah. Currently, stands of Southern Deciduous Forest are primarily restricted to bluff tops and edges adjacent to the St. Croix River and in scattered farm woodlots, which are usually heavily grazed.

Important component trees in this community include red oak, white oak, Hill's oak, and bur oak. In more mesic sites, large-toothed aspen, sugar maple, basswood, and white ash become important. Shrubs indicative of this community include black cherry, common elder, gray dogwood, and hazelnut. Prevalent ground layer vegetation includes dogbane, wild sarsaparilla, rattlesnake fern, tick trefoil, Virginia strawberry, northern bedstraw, wild cranesbill, Jacob's ladder, sweet cicely, wild lettuce, false Solomon's seal, Solomon's seal, wild leek, blue cohosh, goosegrass, bloodroot, large-flowered trillium, and Pennsylvania sedge.

Very few breeding bird species are restricted to or reach their greatest density in the Southern Deciduous Forest in the Valley. Principal breeding species include Cooper's hawk, red-tailed hawk, ruffed grouse, great horned owl, whip-poor-will, common flicker, red-headed woodpecker*, hairy woodpecker, great crested flycatcher, eastern wood pewee, blue jay, common crow, black-capped chickadee, white-breasted nuthatch, house wren, brown thrasher*, American robin, yellow-throated vireo, ovenbird, American redstart, scarlet tanager, rose-breasted grosbeak, indigo bunting, rufous-sided towhee, vesper sparrow (in openings), and field sparrow (in openings).

Deciduous Clear Cuts

A major principle of wildlife management is the provision of a multitude of habitats in various successional stages. Suppression of wildfires and the tremendous reduction of logging that occurred after settlement of the Valley were responsible for allowing many upland sites to return to near climax conditions. Northern Hardwood Forest, dominated primarily by sugar maple and basswood, rapidly becomes prevalent in northern forests that are not managed. Although the mature hardwood forest is a primary habitat for several breeding birds, the lack of early successional stages creates a situation that is relatively unattractive to a number of other species.

Within the last 15 years, foresters and wildlife managers have taken steps to retard succession in several upland forest types. These management practices have been highly successful in providing a variety of successional stage forests and several age classes. Providing a variety of age classes has produced significant beneficial effects for many woodland breeding birds. The primary methods used to accomplish these practices are clear-cutting and selective cutting.

In general, these practices have been accomplished on upland sites in the northern areas of the Central Plain and throughout the Northern Highland. Trembling aspen is the primary tree species associated with Deciduous Clear Cuts. Additional tree and shrub species that are important components of clear cuts include ironwood, hazelnut, sugar maple, and basswood. Important ground layer species include black raspberry, big-leaf aster, rice grass, bottle-brush grass, Pennsylvania sedge, northern bedstraw, bracken fern, and wood anemone. In wet-mesic sites bunchberry and large-flowered trillium are also important.

Deciduous Clear Cuts and associated edge habitat probably support the greatest diversity of breeding birds among the habitats in the Valley. Principal breeding species include ruffed grouse, ruby-throated hummingbird, eastern kingbird, alder flycatcher*, house wren, gray catbird*, brown thrasher, eastern bluebird, golden-winged warbler*, Nashville warbler, yellow warbler, chestnut-sided warbler*, mourning warbler*, common yellowthroat*, Canada warbler*, brown-headed cowbird, rose-breasted grosbeak, indigo bunting*, American goldfinch, white-throated sparrow*, and song sparrow.

Coniferous Communities

Upland Coniferous Forest

Before settlement of the Valley most of the Central Plain and Northern Highland was covered with Upland Coniferous Forest. Logging activities during the late 1800's and early 1900's altered much of this habitat; very few stands of pure Upland Coniferous Forest still exist. Probably the best representative stands occur in and near St. Croix State Park in Pine County and Lucius Woods State Park in Douglas County. In most instances this habitat occurs as small relicts intermixed with several Upland Deciduous Forest species. This habitat type is included because of its past dominance and existing relict stands.

Principal tree species associated with Upland Coniferous Forest are white pine and red pine. Important invaders include white birch, trembling aspen, red maple, sugar maple, black cherry, hazelnut, and ironwood. Prevalent ground layer vegetation includes wood anemone, wild sarsaparilla, big-leaf aster, Pennsylvania sedge, blue bead lily, bunchberry, wintergreen, ground pine, Canada mayflower, partridge berry, starflower, Indian pipe, and dwarf ginseng.

Important breeding bird species of the Upland Coniferous Forest include sharp-shinned hawk, pileated woodpecker, hairy woodpecker, eastern wood pewee, blue jay, common raven, black-capped chickadee, red-breasted nuthatch, hermit thrush, black-and-white warbler, yellow-rumped warbler, pine warbler*, Blackburnian warbler*, ovenbird, purple finch, pine siskin, dark-eyed junco, and chipping sparrow.

Lowland Coniferous Forest

This habitat type occurs in numerous locations north of the Tension Zone. The frequency of the Lowland Coniferous Forest is high but is limited in extent, occurring primarily in three distinct topographic settings: river floodplains, ancient lake beds, and kettles associated with kettle and knob topography in morainal areas. Soils of this habitat are usually acidic and are composed of wet, decaying vegetation that in many instances gives the ground a spongy texture. This habitat type is similar in several respects to the original Boreal Forest. Because most of that habitat type has been destroyed or greatly altered, vegetative characteristics and breeding bird use of the two have been combined.

Principal tree species of the Lowland Coniferous Forest include white spruce, white cedar, balsam fir, yellow birch, black ash, and green ash. Tamarack, American elm, and occasionally red maple, are also important components of this habitat. Shrub layers are usually poorly developed in Lowland Coniferous Forest; green ash and mountain holly are usually the prevalent shrub species. Important species of the ground layer include blue bead lily, bunchberry, creeping snowberry, wintergreen, Labrador tea, Canada mayflower, false Solomon's seal, starflower, blueberry, wild cranberry, round-leaf sundew, downy yellow violet, and sphagnum moss.

Principal breeding birds of this community include pileated woodpecker, yellow-bellied flycatcher, olive-sided flycatcher*, black-capped chickadee, red-breasted nuthatch*, winter wren*, hermit thrush, veery, solitary vireo, black-and-white warbler*, Nashville warbler, northern parula*, magnolia warbler*, yellow-rumped warbler*, ovenbird, northern waterthrush, common yellowthroat, brown-headed cowbird, purple finch*, pine siskin, chipping sparrow, white-throated sparrow, and song sparrow.

Black Spruce–Tamarack Bog

Although not as extensive in distribution as other coniferous or deciduous habitats, bogs are important to a large variety of breeding birds. This community exists primarily north of the Tension Zone and becomes frequent in the Northern Highland. Scattered relict bogs also occur in northern St. Croix and Washington counties. Bogs are formed in ancient lake basins or in outwash associated with morainal deposits. Bog soils are poorly developed and are usually highly acidic, owing in part to anaerobic decomposition of vegetation and temperature.

Black spruce and tamarack are the two most important tree species in this community. Mountain holly and bog birch are the main shrub layer species. Ground-layer vegetation in these bogs is perhaps the characteristic that separates this community from all others. Usually, the most important family is Ericaceae (e.g., leatherleaf, Labrador tea). Herbaceous vegetation in bogs usually contains several carnivorous plants including pitcher plant and round-leaf sundew. Prevalent vegetation includes Labrador tea, leatherleaf, bog rosemary, bog laurel, wild cranberry, buckbean, sphagnum moss, cottongrass, awned sedge, brown sedge, and bluejoint grass.

Principal breeding bird species include olive-sided flycatcher, black-capped chickadee, red-breasted nuthatch, winter wren, veery, black-and-white warbler, Nashville warbler*, yellow warbler, yellow-rumped warbler, common yellowthroat, red-winged blackbird, brown-headed cowbird, purple finch, pine siskin, American goldfinch, chipping sparrow, white-throated sparrow, swamp sparrow, and song sparrow.

Jack Pine Barrens

This community exists throughout the northern portions of the Central Plain and Northern Highland. Extensive stands of Jack Pine Barrens occur on sandy soils associated with the bed of Glacial Lake Grantsburg in Burnett, Pine, and Polk counties. Curtis (1959) considered fire to be an important agent in the origin of Jack Pine Barrens. Soils are primarily sandy and stabilized by various grasses.

Principal tree species of Jack Pine Barrens include jack pine, red pine, Hill's oak, bur oak, large-toothed aspen, and trembling aspen. Sweet fern, New Jersey tea, and blueberry are the most important shrubs of this community. In many areas, blueberry becomes dominant over other shrubs and among the ground layer. Important ground-layer vegetation includes Canada bluegrass, Kentucky bluegrass, pearly everlasting, yarrow, bracken fern, dogbane, big-leaf aster, flowering spurge, whorled loosestrife, wintergreen, and bearberry.

Important breeding birds associated with Jack Pine Barrens are mourning dove, common flicker, blue jay, house wren, American robin, hermit thrush, yellow-rumped warbler, Nashville warbler, ovenbird, northern oriole, brown-headed cowbird, indigo bunting, rufous-sided towhee, chipping sparrow*, clay-colored sparrow, and field sparrow. Recent surveys indicate that the Connecticut warbler is a fairly common breeding species in localized areas of Jack Pine Barrens in northwestern and western Burnett County.

Pine Plantations

This artificial community has become an important avian habitat primarily in St. Croix and Washington counties. Large hectarages of cropland, hillsides, and Old Field Communities have been converted to Pine Plantations. The establishment of this community has accomplished three purposes: soil stabilization, ornamental plantings, and commercial Christmas tree production.

Pine Plantations are primarily monotypic stands of red pine and scotch pine. Occasional stands also include white pine. Size of these plantations usually range from 2 to 20 ha. During the early stages of establishment, ground-layer vegetation retains the character of the original habitat and can consist of Kentucky bluegrass, quackgrass, ragweed, bindweed, Virginia strawberry, and flowering spurge. Continued tree growth, low light, and increased soil acidity results in an almost complete lack of ground-layer vegetation development.

Principal breeding bird species include mourning dove*, blue jay, common crow, house wren, brown thrasher, American robin*, common grackle*, brown-headed cowbird, and chipping sparrow*.

Wetland Communities

Prairie Wetlands

Much of central St. Croix, southern Polk, north central Washington, and south central Chisago counties are dotted with small semipermanent and permanent wetlands. These wetlands occur on glacial outwash associated with the Wisconsin glacial epoch, which ended about 10,000 years ago. Upland soils associated with these wetlands are highly fertile loams and silt loams which are very important for agricultural production. Related to this, large hectarages of Prairie Wetlands have been drained or seriously altered to facilitate expanding agricultural production.

Principal emergent and submerged aquatic vegetation associated with these freshwater, low-acidity wetlands include hardstem bulrush, softstem bulrush, river bulrush, cattail, cane reed, spikerush, burreed, coontail, and water milfoil. Other important species dependent on water permanence and the degree of acidity include arrowhead, water plantain, and reed canary grass.

Characteristic breeding birds associated with Prairie Wetlands include pied-billed grebe*, American bittern*, Canada goose*, mallard*, gadwall*, pintail*, green-winged teal*, blue-winged teal*, ruddy duck*, Virginia rail*, sora*, American coot*, black tern*, tree swallow*, long-billed marsh wren*, yellow warbler, common yellowthroat, yellow-headed blackbird*, red-winged blackbird*, swamp sparrow, and song sparrow.

Forest Bordered Wetlands

Although similar to Prairie Wetlands in geologic origin, Forest Bordered Wetlands are different in flora and fauna. This community is widespread throughout the area north of the Tension Zone. Forest Bordered Wetlands are usually similar in size, but much deeper than Prairie Wetlands, and the interspersion of emergent and submerged aquatic vegetation is less pronounced. Acidity of the water in Forest Bordered Wetlands is generally greater than in Prairie Wetlands. Principal emergent and submerged aquatic vegetation associated with this community includes cattail, wild rice, iris, pickerelweed, arrowhead, water plantain, bladderwort, elodea, coontail, water milfoil, white waterlily, and yellow waterlily.

Characteristic breeding birds associated with these wetlands include common loon*, green heron, mallard, black duck*, wood duck, ring-necked duck*, hooded merganser, Virginia rail, belted kingfisher, tree swallow, long-billed marsh wren, yellow warbler, common yellowthroat, red-winged blackbird, brown-headed cowbird, swamp sparrow, and song sparrow.

Riparian Habitats

The streams and rivers of the Valley are well known for their recreational attractions. Among the important rivers are the Snake, Kettle, Willow, Apple, Clam, Namekagon, and Kinnickinnic. Numerous small streams that are tributaries of these larger rivers often provide excellent trout fishing. Breeding birds associated with streams and rivers may also be included in larger deciduous and coniferous communities. However, nesting strategies of several species are closely related to certain aspects of the ecology of moving water. Principal among these breeding birds are the great blue heron* (locally), mallard, wood duck*, hooded merganser*, spotted sandpiper*, belted kingfisher*, eastern phoebe*, rough-winged swallow*, cliff swallow*, American robin, yellow warbler, common yellowthroat, red-winged blackbird, and song sparrow.

Northern Sedge Meadow

This community occurs throughout the Valley and makes up a large proportion of the aquatic habitats. These wetlands occur primarily north of the Tension Zone. Northern Sedge Meadow usually forms on the bed of an ancient lake or along and adjacent to larger streams and rivers. Soils associated with this community consist primarily of decaying vegetation and have a low mineral content. Groundwater is usually at or near the surface, providing a spongy texture to the soil surface. Probably the largest and best developed examples of Northern Sedge Meadow are associated with the bed of Glacial Lake Grantsburg in Burnett and Pine counties.

Principal vegetation of this community includes foxtail sedge, crested sedge, inland sedge, slender sedge, tussock sedge, fox sedge, cattail, bluejoint grass, manna grass, and dark-green bulrush. Important forbs include marsh cinquefoil, marsh milkweed, purple-stem aster, marsh bellflower, spotted joe-pye weed, meadow sweet, and small bedstraw.

Northern Sedge Meadows do not support the diversity and abundance of breeding birds usually associated with other wetland types. However, several species breed in this community almost exclusively. Principal breeding species include American bittern, mallard, marsh hawk*, ring-necked pheasant, sandhill crane*, sora, common snipe*, short-billed marsh wren*, yellow warbler, common yellowthroat*, red-winged blackbird, brown-headed cowbird, LeConte's sparrow* (local), swamp sparrow, and song sparrow.

Alder Thicket and Shrub Carr

Both Alder Thicket and Shrub Carr communities are similar in geologic origin and flora. One major difference between these habitats is that alder is replaced by willow, particularly silver willow, in Shrub Carrs. Both habitat types are usually associated with ancient lake beds or the floodplains of streams and rivers. In many instances, these habitats develop from the invasion of woody shrubs in a Northern Sedge Meadow. Alder Thicket and Shrub Carr communities occur regularly throughout the Valley. However, there appears to be a predominance of Alder Thickets north of the Tension Zone, and Shrub Carrs occur most frequently within and south of the Tension Zone.

Principal vegetation associated with the Shrub Carr community includes silver willow and red-osier dogwood in the shrub layer. Common grasses and forbs include marsh shield fern, yellowish sedge, bluejoint grass, reed canary grass, manna grass, marsh milkweed, jewelweed, spotted joe-pye weed, water horehound, and meadowsweet. Characteristic breeding birds of Shrub Carr include mallard, blue-winged teal, marsh hawk, ring-necked pheasant*, common snipe, willow flycatcher*, short-billed marsh wren, veery, yellow warbler*, common yellowthroat, red-winged blackbird, brown-headed cowbird, swamp sparrow, and song sparrow.

Vegetation associated with Alder Thicket habitat includes speckled alder and red-osier dogwood in the shrub layer. Characteristic grasses and forbs include dark-green bulrush, tall manna grass, bluejoint grass, marsh milkweed, marsh bellflower, turtlehead, spotted joe-pye weed, jewelweed, field mint, and great water dock. Characteristic breeding birds of Alder Thicket include alder flycatcher*, tree swallow, gray catbird, veery*, golden-winged warbler, yellow warbler, northern waterthrush* (local), common yellowthroat, red-winged blackbird, swamp sparrow*, and song sparrow.

Agricultural Communities

Cropland

One of the most prominent aspects of the landscape in the lower Valley is the presence of agricultural fields. According to figures from the U.S. Department of Agriculture, there were at least 158,540 ha in the Valley devoted to row crop or cereal crop production (row crop = 62.6%, cereal crop = 37.4%) in 1967. By 1977, the totals had increased to 195,587 total ha (73.2% in row crops, 26.8% in cereal crops). Of the nearly 1.8 million ha of the Valley included in this report, 8.8% was devoted to row and cereal crop production in 1967 and 11% in 1977.

During the initial stages of agricultural development, important habitats including native tall grass prairie, deciduous forest, and prairie wetlands were destroyed to accommodate expanded production. Changes in land use of the magnitude attributed to Cropland have had a serious impact on bird populations and bird species diversity. Current agricultural practices of fencerow to fencerow farming, clean farming, fencerow removal, and windbreak removal to facilitate center-pivot irrigation systems, produce additional stresses on bird populations.

Corn, soybeans, oats, barley, and to a limited extent, wheat, are the prominent crops produced in this region. Although a common practice in western Minnesota, summer fallowing the soil has only recently become popular in this region. Characteristic breeding bird species that use Cropland include gray partridge*, killdeer*, horned lark*, western meadowlark, red-winged blackbird, and vesper sparrow.

Hayland

Domestic hay was produced on 128,927 ha in 1967 and 139,393 ha (+7.5%) in 1977. Hayland accounted for 7.2 and 7.8% of the total area of the Valley in 1967 and 1977, respectively. This temporary habitat is important to a variety of early nesting species. Hayland is also important in soil conservation because the soil is not laid bare each year and is not exposed to the ravages of wind and water erosion as it is with row crops. Principal plant species used in hay production include alfalfa, timothy, brome grass, and red clover.

Characteristic breeding birds associated with Haylands include American bittern, mallard, blue-winged teal, pintail, marsh hawk, short-billed marsh wren, bobolink*, eastern meadowlark*, western meadowlark, red-winged blackbird, dickcissel*, savannah sparrow*, grasshopper sparrow*, Henslow's sparrow*, LeConte's sparrow, and song sparrow.

Old Field Community

The Old Field community represents a relatively small proportion of the land area in the Valley. This habitat type develops when land is taken out of agricultural production and allowed to develop by natural succession. Invasion by a variety of plants will result in a rapidly changing vegetational community. Areas of Old Field community are usually no larger than 16 ha; most are 4 to 8 ha.

Characteristic plant species associated with this habitat include a variety of pioneer trees and shrubs, such as trembling aspen, box elder, staghorn sumac, and flowering crab apple. Grasses and forbs associated with this habitat include timothy, awnless bromegrass, Kentucky bluegrass, quackgrass, big bluestem, little bluestem, hoary alyssum, blue vervain, moth mullein, yarrow, evening primrose, common milkweed, alfalfa, goat's beard, sheep sorrel, daisy fleabane, noble goldenrod, and sharp-toothed goldenrod.

Characteristic breeding birds associated with this habitat include American kestrel, mourning dove, eastern kingbird*, brown thrasher, eastern bluebird, golden-winged warbler, yellow warbler, eastern meadowlark, brown-headed cowbird, indigo bunting, American goldfinch, rufous-sided towhee, clay-colored sparrow*, field sparrow*, and song sparrow.

Managed Grasslands

Within the Valley, several thousand hectares of upland fields have been acquired by State and Federal conservation agencies as wildlife management areas or Waterfowl Production Areas. These lands are usually agricultural fields that have been taken out of production. Several different management techniques are used to develop extensive areas of grasses and forbs to provide nesting habitat for a variety of wildlife species.

Characteristic plant species established on Managed Grassland areas include intermediate wheatgrass, switchgrass, timothy, and brome grass. After establishment of these grasses, a number of forbs invade the areas. Several characteristic invaders include hoary alyssum, yarrow, blue vervain, daisy fleabane, and sharp-toothed goldenrod.

These established communities provide habitat for a variety of species including American bittern, mallard, pintail, blue-winged teal, marsh hawk, ring-necked pheasant, short-billed marsh wren, common yellowthroat, bobolink, eastern meadowlark, western meadowlark, red-winged blackbird, dickcissel, and savannah, grasshopper, Henslow's, vesper, and song sparrows.

Residential Habitats

Small towns and cities scattered throughout the Valley provide a diversity of habitats for breeding birds. Intermixed with concrete buildings are areas of hedgerows, row trees, tree groves, lawns, and parks. Diverse food sources, ranging from feed mills and lawns to gardens and bird feeding stations, add to the vegetation available for breeding birds.

Characteristic birds associated with Residential Habitats include rock dove*, mourning dove, screech owl, common nighthawk*, chimney swift*, downy woodpecker, purple martin*, blue jay, black-capped chickadee, white-breasted nuthatch, house wren, gray catbird, brown thrasher, American robin, starling*, house sparrow*, northern oriole, common grackle, cardinal, rose-breasted grosbeak, and American goldfinch.

Methods, Terminology, and Nomenclature

The counties covered in this report include Chisago, Pine, and Washington in Minnesota and Burnett, Douglas (part), Pierce, Polk, and St. Croix in Wisconsin. References made to a species status or occurrence in the Valley will pertain to these counties. Ideally, a complete coverage of the birds occurring in this region would include records for all counties within the watershed. However, because many records are not discernible to exact locations within a county (in or out of the watershed) I have, for conformity, included bird records only for counties that border on the St. Croix River.

Foremost among the published sources of data on bird occurrence and distribution presented in this report were the *Loon* and its predecessor, the *Flicker*, the quarterly publication of the Minnesota Ornithologists Union, and the *Passenger Pigeon*, the quarterly publication of the Wisconsin Society for Ornithology. Important papers dealing with species or species groups have been published in these journals and extensive use was made of the data contained therein. Considerable use was made of published reports in *American Birds*, the field report publication of the National Audubon Society. Probably the most important contribution of *American Birds* to the present report was the yearly publication of Christmas Bird Counts (CBC) conducted in both States.

I conducted field work in this region from 1966 through 1978, and intermittently during 1979–80. Before 1969, most observations were made in northern Polk, southern Douglas, Burnett, and eastern Pine counties. During 1969–76, field work was expanded to include the remainder of the counties and intensive observations were started on several species in Pierce, St. Croix, and Washington counties. Many of the dates of occurrence and statements on abundance and distribution were derived largely from my unpublished field notes. The unpublished field notes of Rev. Samuel Robbins for 1960–68 in St. Croix, Polk, and Pierce counties were also examined extensively. Several State parks and wildlife management areas in both States were visited and some limited data (with the exception of the Crex Meadows Wildlife Area) were made available.

Data on breeding and winter status were gathered from three sources. First, intensive field work by several previous investigators and me led to the discovery of numerous nests or dependent young. These observations provide the foundation for species status remarks and habitat use of breeding birds. Secondly, the U.S. Fish and Wildlife Service, Migratory Bird and Habitat Research Laboratory, Laurel, Maryland, has established a number of BBS transects throughout North America (Robbins and Van Velzen 1967). These 39.2-km transect routes are selected at random and are censused once each year during June. Five transect routes were established in the Valley; unfortunately, all five are in Wisconsin (Fig. 4). Data from these routes are presented to point out regions of peak populations of several species and, in some instances, to show geographic differences in species breeding distribution. Third, CBC sponsored by the National Audubon Society provide an important source of data on winter bird populations and geographic differences in species abundance. At least eight CBC areas have been established within the Valley. However, only five (Fig. 5) have been

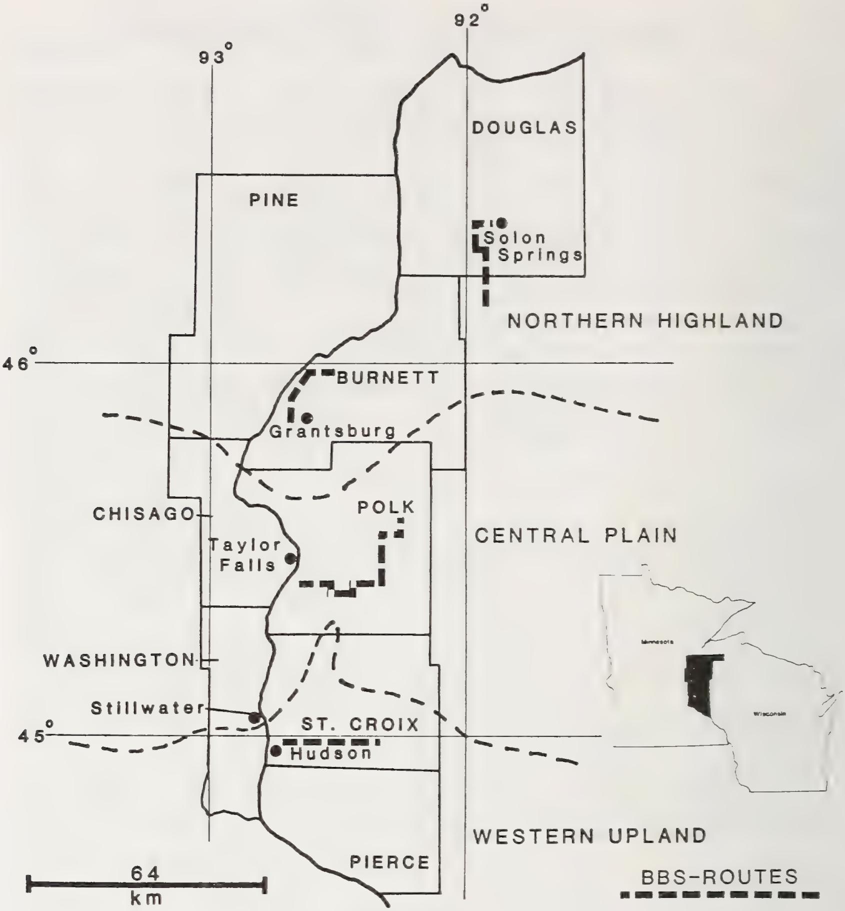

Fig. 4. Location of Breeding Bird Survey routes in the St. Croix River Valley.

counted for a sufficient number of years to allow meaningful comparisons.

Terms

Considerable conjecture and argument has developed about what is the best method for describing a species occurrence, regularity, and abundance. Terms are treated under three categories: status, season, and abundance. The terms used to describe each species status in the present report are adapted from those presented in Green and Janssen (1975), including

Regular—A species that occurs at some location in the Valley during at least one season each year.

Casual—A species expected to occur at least once every 3 to 5 years, but not annually.

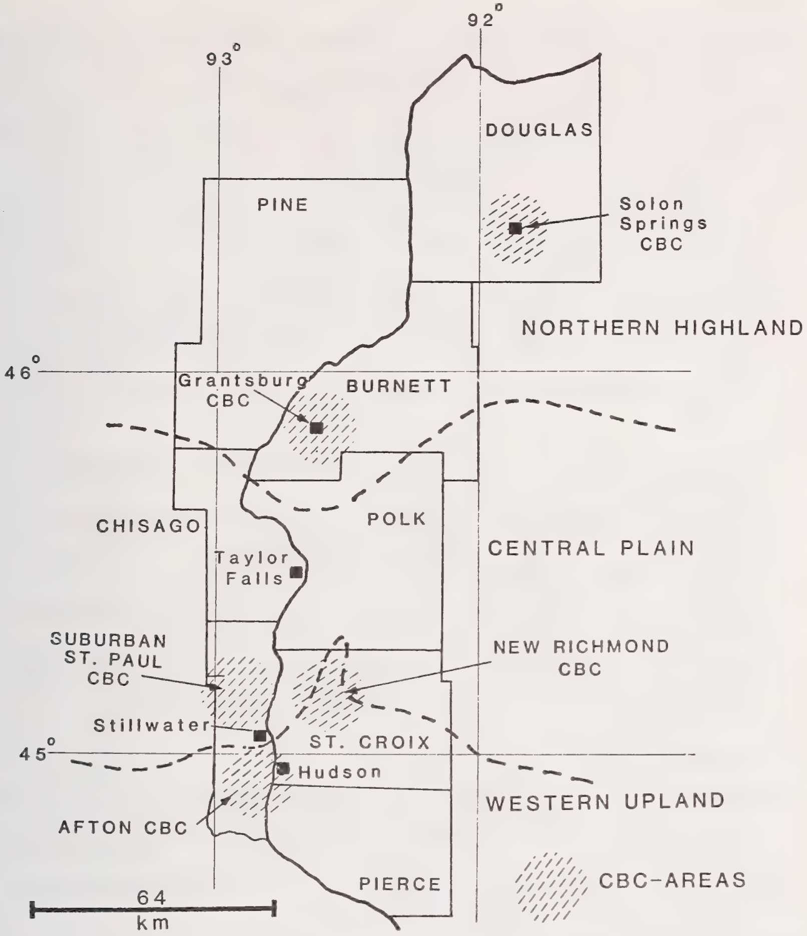

Fig. 5. Location of major Christmas Bird Count areas in the St. Croix River Valley.

Accidental—A species that is not expected to occur again or that occurs very infrequently.

Hypothetical—A species that probably occurred in the Valley at least once, but the circumstances of the observation leave the record in doubt.

Introduced—A species that is naturally foreign to this region but has been released in the area as an act of man and is now established and reproducing without additional influence by man.

Extirpated—A species that once occurred naturally in the Valley, has now been eliminated, but still exists elsewhere. This term applies to both migrants and nesting species.

Extinct—A species that no longer exists anywhere on earth.

The population status of several species has recently become a concern of the public. Legal protection for all birds except the rock dove, starling, and house sparrow has been provided by the Federal Government by the Migratory Bird Treaty Act of 1918, as amended (40 Stat. 755; 16 U.S.C. 703-711). Eagles have been afforded additional protection by the Eagle Act of 1940 (54 Stat. 250; 16 U.S.C. 668). Several species have been given even greater protection by the Federal Endangered Species Act of 1973 (87 Stat. 884; 16 U.S.C. 668aa-668cc). Both Minnesota and Wisconsin have enacted special legislation within their respective States that provides statewide protection for species that are declining locally or regionally, but not on a level to be afforded protection by the Endangered Species Act of 1973.

Official lists of protected bird species have been prepared for Minnesota and Wisconsin. Forty-three of the species listed by either State have been recorded in the Valley (Table 1). Terms used throughout this report to describe the special status of these species are adapted from Les (1979) and Moyle (1980).

Endangered—A species whose continued existence is in jeopardy and is provided special protection by law.

Threatened—A species that appears likely to become endangered. Threatened species are provided special protection by law.

Watch—A species for which some problem of abundance is suspected but not proven. The purpose of this classification is to focus attention on a species before it becomes threatened or endangered. This is an informal classification and no additional legal protection is provided. In Minnesota, species in this classification are considered *Priority.*

Terms used in describing the occurrence of a species in the Valley include

Permanent resident—A species that is largely nonmigratory or, if migratory, only a very small proportion of the population departs during a migration period.

Migrant—A species that normally occurs in the Valley only during the well-defined spring and fall migration period.

Nesting species—A species for which a viable clutch of eggs, dependent young in the nest, or young that have left the nest but are still dependent have been observed.

Summer resident—A species that occurs in the Valley during the normal nesting period and in all likelihood nests, but for which there are no confirmed records of eggs or dependent young.

Winter resident—A species that winters even though greater numbers may occur during migration.

Terms used in relating the relative abundance of each species during migration, winter, or the breeding season relate to its importance to the total avifauna. These terms adapted from Stewart (1975) are described as follows:

Abundant—A species that, because of its habits and conspicuousness, occurs in very large numbers.

Common—A species that occurs in large numbers.

Fairly common—A species that occurs in fair to moderate numbers.

Uncommon—A species that is found in low numbers.

Table 1. *Endangered (E), threatened (T), priority (P), and watch (W) species in the St. Croix River Valley.*

Species	Minnesota	Wisconsin
Common loon		W
White pelican	P	
Double-crested cormorant		E
Great egret		T
Snowy egret	P	
Great blue heron		W
Black-crowned night heron		W
Yellow-crowned night heron	P	
Black duck		W
Red-breasted merganser		W
Cooper's hawk		T
Marsh hawk	P	W
Red-shouldered hawk		T
Bald eagle	T	E
Osprey		E
Peregrine falcon	E	E
Merlin	P	W
Spruce grouse		W
Sharp-tailed grouse		W
Greater prairie chicken	P	T
Bobwhite	T	
Yellow rail	P	W
King rail	T	
American avocet	P	
Piping plover	T	E
Marbled godwit	P	
Upland sandpiper	P	W
Common tern	P	E
Forster's tern		E
Caspian tern		W
Black tern		W
Great gray owl	T	
Short-eared owl	P	
Common flicker		W
Black-backed three-toed woodpecker	P	
Bewick's wren		W
Eastern bluebird	P	W
Loggerhead shrike		T
Dickcissel		W
Grasshopper sparrow		W
Baird's sparrow	P	
Sharp-tailed sparrow	P	
Vesper sparrow		W
Field sparrow		W

Rare—A species whose range includes the Valley but is recorded in low numbers.

Very rare—A species that occurs in such low numbers that it is of minor importance.

Table 2. *Classification of wetland types in the St. Croix River Valley. This classification follows Cowardin et al. (1979) and Curtis (1959).*

Wetland name used in this report	Wetland type (Shaw and Fredine 1956)	Water chemistry	Authority
Temporarily flooded	1	Fresh	Cowardin et al.
Northern sedge meadow	2	Fresh	Curtis
Seasonally flooded	3	Fresh	Cowardin et al.
Semipermanently flooded	4	Fresh	Cowardin et al.
Permanently flooded	5	Fresh	Cowardin et al.
Shrub carr	6	Fresh	Curtis
Bog	8	Acidic	Curtis

Nomenclature

The taxonomic treatment of birds presented in this report follows the American Ornithologists' Union (AOU) *Check-list of North American Birds* (1957), and the 32nd (AOU 1973) and 33rd (AOU 1976) supplements to the Check-list. One deviation from the AOU standard sequence is presented for the shorebirds. In this instance, I followed the sequence recommended by Jehl (1968).

Description of the major plant communities of the Valley follows Curtis (1959). Major habitats used by each species were determined from personal field investigations and from published reports. The taxonomic names of plants described in the habitat sections are those used in Gleason and Cronquist (1956). Common names of some plant species, primarily grasses and sedges, are taken from Britton and Brown (1913). Voucher specimens of most of the important grasses and forbs used in this report are housed in the Herbarium, Department of Biology, University of Wisconsin—River Falls.

The wetland classification used in this report (Table 2) is a combination of the systems developed by Cowardin et al. (1979) and Curtis (1959). Cowardin et al. (1979) employ a hierarchical system with modifiers for water regime, water chemistry, and soil type. Three wetland types (Northern Sedge Meadow, Shrub Carr, and Bogs) were named and classified by Curtis (1959). Because these names are widely used and accepted in the Valley, I have deviated from Cowardin's system in that instance.

Species Accounts

FAMILY GAVIIDAE: Loons

Common Loon (*Gavia immer*)

Status: Regular migrant and nesting species.

Migration: Common (locally abundant) during spring and fall throughout the Valley. Spring migrants arrive in the Western Upland during the first week of April (earliest—4 April 1964, St. Croix County; Soulen 1965) and the Northern Highland 10–15 April. Peak spring abundance occurs 20 April to 1 May. During this period flocks of 5 to 10 birds are common and flocks totaling 15 to 20 are occasional on larger lakes. Spring departure from the southern one-third of the Valley occurs by 15 May. Fall migrants arrive in the Western Upland during the first week of October and remain until water on the larger lakes freezes in late November. No major common loon staging areas exist in this region, resulting in relatively small numbers observed during the fall.

Nesting Season Distribution: Uncommon nesting bird on larger lakes and marshes of the Northern Highland, rare and local in the Central Plain. Casual summering birds near Roberts, St. Croix County, indicate possible nesting although no broods have been observed. Longley (1949) reported a pair with one young in Washington County on 17 June 1949. Additional Washington County brood records were obtained in 1970 and 1971 (Eckert 1971).

Habitat: Common loons are primarily a species of large permanently flooded wetlands, particularly those containing small islands. Most wetlands used for nesting are bordered by deciduous forest, chiefly trembling aspen and maple, and contain peripheral zones of emergent aquatic vegetation. At the Crex Meadows Wildlife Area in Burnett County, common loons nest on semipermanently and permanently flooded wetlands. The vegetation consists primarily of cattail and various species of sedge. Evrard et al. (1978) found that common loons at Crex Meadows occupied wetlands that ranged from 6.9 to 324 ha.

Concern has been expressed recently about the population status of this species in Wisconsin, Minnesota, and other northern States. The primary threat to the nesting habitat of this species is shoreline development surrounding nesting lakes.

Red-throated Loon (*Gavia stellata*)

Status: Casual migrant; one summer record.

Records: Spring records include Pierce County—10 May 1967; St. Croix County—25 April 1962 and 17 May 1965; Burnett County—15 May 1950 (Robbins 1950*b*). During the summer of 1953 a nonbreeding red-throated loon was observed on 11 June and 17 July at Crex Meadows Wildlife Area, Burnett County.

FAMILY PODICIPEDIDAE: Grebes

Red-necked Grebe (*Podiceps grisegena*)

Status: Regular migrant and nesting species.

Migration: Rare spring and fall migrant in the Western Upland, casual or absent elsewhere. Spring migrants arrive during the second week of April (earliest—8 April 1959, Burnett County). Dates of peak abundance cannot be determined because of low numbers. Nonbreeding migrants have departed by 20 May. The first fall migrants arrive 25 September to 5 October and the last depart by 1 November (latest—10 November). During both seasons migrants are usually observed in central St. Croix County and at several areas along the St. Croix River in Washington, Polk, and St. Croix counties.

Nesting Season Distribution: The red-necked grebe is a very rare and local nesting species. Green and Janssen (1975) showed a nesting record for Washington County. Apparently this species no longer nests on the Minnesota side of the St. Croix River. Presently, nesting occurs only on prairie wetlands in central St. Croix and extreme southern Polk counties.

The first nesting for the Valley in Wisconsin was recorded in 1973 from East Twin Lake near Roberts. During the summer of 1976, three pairs produced young on Twin Lakes and an additional pair was successful on Oakridge Lake near New Richmond. In 1977, four pairs produced young on Oakridge Lake, one pair on East Twin Lake, and a sixth pair produced young on a small wetland near Star Prairie in Polk County. During 1978–79 breeding populations were greatly reduced with activity restricted to Oakridge Lake (M. Schmidt, personal communication).

Habitat: All 12 nesting records have been obtained on semipermanently and permanently flooded wetlands. These wetlands range in size from 8.5 to 93 ha. Extensive beds of submerged aquatic plants are present on these wetlands. All nests have been located in large beds of softstem bulrush.

Horned Grebe (*Podiceps auritus*)

Status: Regular migrant, casual nesting species.

Migration: Common migrant throughout the Valley. Spring migrants begin to arrive in the Western Upland during the second week of April (earliest—24 March) and the Northern Highland 1–5 May. Peak abundance occurs during the first week of May and departure by 15 May. Fall migrants begin to arrive during the third week of September. Peak abundance occurs about 15 October when occasional flocks of 50 to 60 individuals are observed on larger lakes. Fall migrants have departed by November 20.

Nesting Season Distribution: One nesting record exists for this region. On 2 July 1951 an adult with a brood of four was observed at the Crex Meadows Wildlife Area, Burnett County. On 14 June 1974, I observed an adult in breeding plumage near Range, Polk County.

Habitat: Horned grebes use a wide range of wetland classes including seasonally, semipermanently, and permanently flooded wetlands. In the Northern Highland, extensive use is made of Forest Bordered Wetlands and occasional use is made of acidic bog wetlands and larger rivers. The Burnett County nesting pair were using a large sedge meadow wetland.

Eared Grebe (*Podiceps nigricollis*)

Status: Regular spring and casual fall migrant; four summer records.

Migration: Rare migrant in the Western Upland and Central Plain. There are no records except from Crex Meadows in the Northern Highland. Spring migrants begin to arrive during the last week of April (earliest—20 April 1975, Polk County) and remain through 5 June. Sightings are most often of single or paired birds. Dates for fall migrants are too few to establish a pattern. Fall observations are rare, noted between 10–20 September.

Nesting Season Distribution: One nesting record exists for the Valley. S. D. Robbins found an adult carrying young on its back during the summer of 1968 on East Twin Lake near Roberts, St. Croix County (Robbins 1969*a*). This is the only known nesting record of the eared grebe in Wisconsin. On 21 July 1952, three eared grebes were observed on Phantom Lake, Crex Meadows, and on 12 July 1956, a single bird was observed at Crex Meadows (Lound and Lound 1956*b*). During the summer of 1977, a single adult remained on Oakridge Lake, St. Croix County, until 8 August.

Habitat: Eared grebes in the Valley have been found primarily on large permanently flooded wetlands with extensive growths of emergent and submerged aquatic vegetation. The St. Croix County nesting pair used a large semipermanently flooded wetland. Vegetation of that wetland was characterized by extensive beds of coontail surrounded by hardstem bulrush and cattail.

Western Grebe (*Aechmophorus occidentalis*)

Status: Casual migrant.

Records: Western grebes have been observed twice in spring and once in fall at Crex Meadows, Burnett County. The first record was 30 May 1974, and the second 8 June 1976. The fall observation was on 26 August 1975. All Crex Meadows records were obtained from the Phantom Lake flowage. J. O. Evrard observed a single western grebe on the Fish Lake Wildlife Area near Grantsburg, Burnett County, on 3 June 1979. This bird was observed on Crex Meadows on 11 June 1979 (Tessen 1979*b*). This species has been recorded three times in St. Croix County: 2 October 1976, two birds on Oakridge Lake near New Richmond; 6 October 1967, three birds on Cedar Lake near Star Prairie; and 12 October 1974, on Oakridge Lake.

Pied-billed Grebe (*Podilymbus podiceps*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Western Upland and Central Plain, fairly common in the Northern Highland. Spring migrants arrive during the last week of March (earliest—9 March 1957, Burnett County). Peak abundance occurs 20 April to 1 May. During peak migration, concentrations of 75 to 100 individuals occur on several larger lakes in Chisago, Polk, and Burnett counties. Fall migrants begin to concentrate in early September. Peak fall abundance occurs during the second week of October and departure by 10 November (latest—19 December 1974, Pierce County).

Nesting Season Distribution: Common nesting species throughout the Valley. The largest numbers occur on prairie wetlands of the Central Plain and in the extensive marshes of southwestern Burnett County.

Habitat: The pied-billed grebe occurs most commonly on seasonally and semipermanently flooded wetlands with lush stands of emergent aquatics; cattail and bulrush appear to be preferred for nesting. Nesting pied-billed grebes are also found on large permanently flooded and Alder Thicket wetlands in the Northern Highland. Breeding populations in these habitat types are lower than on seasonally or semipermanently flooded wetlands.

FAMILY PELECANIDAE: Pelicans

White Pelican (*Pelecanus erythrorynchos*)

Status: Casual migrant.

Distribution: White pelicans have been observed in the Valley at least 10 times: St. Croix County—28–30 April 1941 (Schorger 1954), May 1950, and 2–6 November 1975 (Lesher 1976). Polk County—23 April 1867 (Schorger 1954), and 24 April to 12 June 1947. Burnett County—10 July 1970 (Crex Meadows files), and 30 October 1883 (Schorger 1954). Washington County—16 April 1976. Chisago County—about 60 white pelicans were observed migrating upstream at Taylor's Falls on 14 April 1979 (Turner 1979). Pine County—18 September 1972 (M. Link, personal communication).

Habitat: Most records of white pelicans have been of birds using large lakes, man-made impoundments, or open stretches of the St. Croix River.

FAMILY PHALACROCORACIDAE: Cormorants

Double-crested Cormorant (*Phalacrocorax auritus*)

Status: Regular migrant and nesting species. The Wisconsin Department of Natural Resources (WDNR) has listed this species as endangered (Les 1979). Loss of nest trees, use of pesticides, and human disturbance are listed as reasons for their decline.

Migration: Rare and local migrant throughout the Valley. Formerly a common to abundant migrant throughout its range, populations of double-crested cormorants have experienced alarming declines. Records exist of "flocks of thousands" migrating north along the Mississippi and St. Croix rivers until the 1950's. Currently, observers are fortunate to find more than 25 individuals during the year. The average date of spring arrival is 18 April (earliest—4 April 1976, Chisago County). Peak spring migration occurs 25 April to 10 May, and departure from nonbreeding areas by 25 May. Peak fall migration occurs between 10–20 September and departure by 15 October (latest—3 November 1975, Burnett County).

Nesting Season Distribution: Double-crested cormorants are rare and local during the nesting season in this region, currently known to nest only at the Crex Meadows and Fish Lake Wildlife Areas in Burnett County. The first nesting was noted at Crex Meadows in 1968. This colony was in a heron rookery on Phantom Lake. Because of degredation of nesting trees, the Phantom Lake colony declined, and birds moved to the Grettum Flowage at Fish Lake Wildlife Area. In 1973, 23 nests were observed in the Grettum Flowage colony.

Habitat: Both Phantom Lake and Grettum Flowage are large impoundments characterized by deep water and dead trees. This temporary habitat type was created when tree growth in these basins was inundated by rising impounded waters. Construction of nest platforms in the Phantom Lake colony has attracted several breeding pairs. This management practice may prove essential in the maintenance of these two colonies.

FAMILY ARDEIDAE: Herons and Bitterns

Great Blue Heron (*Ardea herodias*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Common migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive in the Western Upland about 10 March (earliest—1 March 1969, St. Croix County) and reach the Northern Highland by 1 April. Peak migration occurs 5-20 April. Fall migration begins in mid-July with the gradual dispersal of young from rookeries. Peak fall migration occurs 25 August to 30 September and most depart by 10 November (latest—20 November 1964 and 9 December 1971, Burnett County).

Nesting Season Distribution: Fairly common and local nesting species throughout the Valley. Evidence of nesting has been documented in all counties except Pierce. The two largest rookeries in the region are at Crex Meadows Wildlife Area, Burnett County, and at Pine Lake, Pine County. At least four rookeries were active in Burnett County in the late 1940's and early 1950's (Williams 1957). The Crex Meadows rookery located on Phantom Lake was first used in 1952 (Williams 1957). Further records related to the breeding population of this rookery follow:

1958—157 active nests
1960—108 active nests
1962—109 active nests
1968—160 active nests. Rainstorm (8.5 cm) on 30 June left 65 nests in the rookery. About 150 herons were found dead near the rookery.
1973—169 active nests, Phantom Lake; 13 active nests, North Fork Flowage
1974—143 active nests in four rookeries
1975—75 active nests in the Phantom Lake rookery
1976—31 active nests

Deterioration of nest platform trees is the primary cause of the rookery decline at Crex Meadows. Attempts at placing artificial nest platforms for great blue herons on the Phantom Lake rookery have been successful in attracting double-crested cormorants. However, the great blue herons have not reestablished to former levels.

Winter: Three winter records exist for St. Croix County: 2 January 1961; 1 January 1971; and 1 January 1972. All birds were recorded on the Afton CBC.

Habitat: Most nesting rookeries in this region exist as small colonies built on dead or dying deciduous trees near natural lakes. The Burnett County colonies are in decaying trees associated with man-made impoundments. As evidenced by the continual changes in colony size and location of breeding populations at Phantom Lake, these temporary habitats are in a constant state of deterioration. In the Western Upland, several small rookeries exist in living green ash and American elm associated with the Lowland Deciduous Forest community. One rookery in the Northern Highland is in living white pine trees close to the St. Croix River in Burnett County.

Green Heron (*Butorides striatus*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland, primarily on the prairie wetlands of St. Croix, Washington, and southern Polk counties. Fairly common in the Central Plain, and uncommon and local in the Northern Highland. Spring migrants begin to arrive during the last week of April (earliest—6 April 1975 and 12 April 1964, Washington County). Average date of first arrival in Burnett County is 10 May, reaching Douglas County by 15 May. Peak spring abundance occurs 5–20 May. Fall migration begins in mid-August with formation of loose flocks. Peak fall movements occur 1–15 September. Green herons depart the Northern Highland by 15 September and the Western Upland by 10 October (latest—27 October 1975 and 9 November 1965, Washington County).

Nesting Season Distribution: Fairly common nesting species in the Western Upland, particularly the prairie wetland region of St. Croix, Washington, and southern Polk counties. Uncommon in the Central Plain, and rare and local in the Northern Highland. Substantial breeding populations occur in the marshes of Glacial Lake Grantsburg in Burnett County. Roberts (1932) cited a June 1919 nest containing three young in Pine County. Documented breeding records exist for all counties in the river valley except Chisago and Douglas. Jackson (1941) failed to record this heron during the 1919 breeding season in northwestern Wisconsin.

Habitat: Breeding green herons utilize a variety of habitats for nesting. In the Western Upland, breeding pairs and nests are typically observed in seasonally, semipermanently, and permanently flooded wetlands, and riverine habitats. In the Central Plain, breeding green herons are found typically in seasonally and semipermanently flooded wetlands, but also occupy Shrub Carr wetlands with a scattering of open water areas.

Little Blue Heron (*Florida caerulea*)

Status: Accidental, one record.

Record: One adult was seen near Dunroven, Washington County, on 23 April 1962 (Huber 1962). Because of the recent noticeable expansion of this species in the upper Midwest, I would expect this species to be recorded more regularly in the future.

Cattle Egret (*Bubulcus ibis*)

Status: Casual migrant.

Records: The first cattle egret record for the Valley was obtained in Chisago County on 7 May 1971, when six birds were observed. One was observed in Washington County on 25 April 1977 (Savaloja 1977). In Pierce County a single bird was observed near River Falls on 28 April 1976. At Crex Meadows, Burnett County, groups of four birds each were observed on 24–28 May 1974 and 16 April 1976. J. O. Evrard reported that cattle egrets were present during July 1979 at Crex Meadows (Tessen 1979*b*).

Great Egret (*Casmerodius albus*)

Status: Regular migrant and nesting species. The Wisconsin DNR has listed this species as threatened (Les 1979). Wetland drainage, loss of mature nest trees, pesticides, and human disturbance are listed as reasons for the decline.

Migration: Uncommon migrant in the Western Upland, rare and local in the Central Plain. Except in the vicinity of Crex Meadows, Burnett County, this species is rare north of a line extending from Chisago to northeastern St. Croix counties. First spring migrants arrive in the Western Upland 10–15 April (earliest—29 March 1968) and in Burnett County about 20 April. One Polk County record was obtained on 10 April 1970. Fall migration begins in mid-August. Peak fall populations occur 25 August to 10 September and departure by 10 October (latest—30 October 1970 and 31 October 1956, Burnett County).

Nesting Season Distribution: Rare and local nesting species with documented breeding records from Washington, St. Croix, and Burnett counties. Establishment of this bird as a breeding species has been fairly recent. Jackson (1941) failed to observe great egrets during 1919 in northwestern Wisconsin. Roberts (1932) described the great egret as "occasionally a straggler from the south," yet cites no records from the Minnesota counties. The first record for the Valley is provided by King (1949), who reported this species at Prescott, Pierce County, in 1946. Great egrets were first reported at Crex Meadows, Burnett County, in 1948. Later, summer observations ranged from 19 in 1956 to 1 in 1969. Nesting at Crex Meadows was first recorded on 25 June 1975 (Evrard 1975). Since 1975, a small nesting colony has remained on the Fish Lake Wildlife Area, Burnett County. In Washington County, nesting has been established with a colony of undetermined size (Green and Janssen 1975). St. Croix County breeding records were established in 1976 when two young were seen feeding with adults along Ten Mile Creek on 11 July. These birds nested in a small great blue heron colony along the

Willow River near New Richmond.

Habitat: Washington and St. Croix county colonies exist in live trees of Lowland Deciduous Forest. Nests at Fish Lake Wildlife Area occur in jack pine trees killed by the rising waters of Grettum Flowage.

Snowy Egret (*Egretta thula*)

Status: Accidental, one record.

Record: Norman Stone observed a single snowy egret at Crex Meadows, Burnett County, on 4 and 5 May 1959 (Stone 1959*a*).

Louisiana Heron (*Hydranassa tricolor*)

Status: Accidental, one record.

Record: One Louisiana heron was observed at Crex Meadows, Burnett County, on 7 July 1977 (Tessen 1977).

Black-crowned Night Heron (*Nycticorax nycticorax*)

Status: Regular migrant and nesting species.

Migration: Uncommon and local migrant in the Western Upland, rare in other regions. Spring migrants arrive in the Western Upland 10–15 April, reaching peak abundance 1–10 May. Average date of spring arrival in Burnett County is 10 May. Fall migration begins 25 August to 1 September and departure by 1 October (latest—28 November 1967, Washington County).

Nesting Season Distribution: Rare and local nesting species. Confirmed breeding records have been reported only from St. Croix and Burnett counties; however, several summer observations have been made in Washington County. Roberts (1932) stated that one of the most northerly colonies in Minnesota occurred on the St. Croix River in Pine County. Unfortunately no dates or locations are provided.

Habitat: Three nesting colonies of black-crowned night herons are known in this region. Habitats associated with these colonies include wetland habitat dominated by bulrush and cattail. In proximity are small groves of alder and willow used for nest platforms.

Yellow-crowned Night Heron (*Nyctanassa violacea*)

Status: Accidental, one record.

Record: Green and Janssen (1975) cite a 6 June 1964 record from St. Croix State Park, Pine County.

Least Bittern (*Ixobrychus exilis*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant in the Western Upland and Central Plain. First spring migrants arrive 5–10 May and are most frequently observed 20–25 May. Fall migration begins 15–25 August and departure by 25 September.

Nesting Season Distribution: Uncommon nesting species in the Western Upland, uncommon to rare and local in the Central Plain. Documented breeding records exist for St. Croix County (three nests), Polk County (one nest), and Burnett County (one nest). Summer observations of adults in Chisago and Washington counties provide inferred evidence of nesting in those counties.

Habitat: Principal nesting habitat of the least bittern includes semipermanently and permanently flooded wetlands. Nests observed in St. Croix and Polk counties were in extensive stands of hardstem bulrush and river bulrush. The Burnett County nest was in a mixed stand of cattail and river bulrush.

American Bittern (*Botaurus lentiginosus*)

Status: Regular migrant and nesting species, accidental in winter.

Migration: Fairly common spring and fall migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive 10–20 April (earliest—4 April 1974, Burnett County), reaching peak abundance 1–5 May. Fall migration begins about 15 August in the Northern Highland and 25 August to 1 September elsewhere. Peak numbers occur 1–20 September. Departure from the Northern Highland occurs 20 September to 1 October; departure elsewhere is 10–25 October.

Nesting Season Distribution: Fairly common and well distributed in all regions. Breeding pairs occur with greatest frequency in the prairie wetland region of St. Croix, Polk, and Washington counties, and at Crex Meadows, Burnett County. Documented nest records exist for St. Croix, Polk, Burnett, and Washington counties. Evidence of nesting exists for the remaining counties. Jackson (1941) reported flushing one American bittern from a marsh at the headwaters of the St. Croix River in Douglas County on 8 August 1919.

Winter: Wayne Norling observed a single bird at Crex Meadows, Burnett County, on 9 January 1976.

Habitat: American bittern breeding habitat use varies with geographic province. Typical breeding habitat in Western Upland includes seasonally, semipermanently, and permanently flooded wetlands. Vegetation associated with these wetlands includes river bulrush, cattail, softstem bulrush, hardstem bulrush, and phragmites. Preferred habitat in the Central Plain is similar with a higher percentage of reed canary grass in seasonally flooded wetlands. Occasionally this species uses upland fields including Haylands, oat fields, Managed Grasslands, and retired cropland for nesting. In the northern regions of the Central Plain and throughout the Northern Highland, breeding habitat includes cattail–bulrush marshes. A high percentage of breeding pairs occur in sedge meadows in this region, as well as edges of Black Spruce–Tamarack Bog and northern Forest Bordered Lakes.

FAMILY ANATIDAE: Swans, Geese, and Ducks

Whistling Swan (*Olor columbianus*)

Status: Regular migrant, two summer records.

Migration: Common to locally abundant spring migrant in the Western Upland, fairly common in the Central Plain and uncommon in the Northern Highland. Spring migrants arrive about 25 March in the Western Upland and by 15 April in the Northern Highland. Peak spring migration occurs 10–25 April. During this period, flocks of 300 to 400 birds are frequently observed, primarily on the prairie wetlands of St. Croix and Washington counties. Roberts (1932) cited the passage of about 2,000 whistling swans through the Valley during "the spring of 1923." Departure is very rapid; most birds are gone by 10 May (latest—13 May 1975, Burnett County).

Fall migration begins with the arrival of the first birds in the Northern Highland about 5 October. Small groups of swans slowly move into the region during most of October. Peak fall migration occurs 25 October to 15 November. Currently, peak concentrations range from 100 to 300 individuals. Roberts (1932) described the observation of "several mixed flocks of swans and geese, one numbering 1,200 to 1,500 birds" at Stillwater. Dates of peak numbers vary considerably and are dependent upon the advancement of northern cold fronts. Departure from the region usually occurs by 1 December and is dependent upon the amount of ice formed on area waters.

Summer: A lone whistling swan was observed at Crex Meadows, Burnett County, on 26 June 1957 (Lound and Lound 1957*d*). A single bird remained in St. Croix County during the 1979 summer (Tessen 1979*b*). Both birds were probably injured.

Habitat: Migrant whistling swans utilize a variety of wetland types during migration. In spring, whistling swans are usually found feeding in numerous temporarily flooded wetlands which are fertile. Larger semipermanently and permanently flooded wetlands are used in spring, primarily as roosting sites. During fall migration swans utilize the larger permanently flooded wetlands and open riverine habitats.

Canada Goose (*Branta canadensis*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Common to locally abundant migrant throughout the region, especially numerous along the St. Croix River and in central St. Croix, Washington, and southern Burnett counties. Arrival of the first spring migrants in the Western Upland occurs 20–25 February and they have reached the Northern Highland (Burnett County) by 10 March. Peak spring migration occurs 25 March to 20 April. Largest numbers of migrants usually occur at the Crex Meadows Wildlife Area, Burnett County.

Fall migration begins about 1 September with the formation of loose flocks among local breeding birds. A gradual influx of migrants adds to the population, and peak fall migration occurs 15 October to 5 November. The largest concentration on record is 8,000 at Crex Meadows on 31 October 1970. The fall population rapidly declines after the peak and most birds have departed by 10 December.

Nesting Season Distribution: Currently a fairly common nesting species throughout the region, common at Crex Meadows. The success of the Canada goose as a nesting bird is related to the reestablishment of breeding adult giant Canada geese (*B. c. maxima*) at Afton, Washington County, and at Crex Meadows. A captive flock was established at Crex Meadows in 1957, and the first young were produced in the wild in 1960. This flock steadily increased and now over 100 pairs produce 300 young annually (WDNR files).

The Afton flock was established in 1960 and resulted in movement of breeding birds into nearby wetlands of Washington, Polk, and St. Croix counties. Canada geese were first recorded summering in St. Croix county in 1961 and nesting was recorded in 1963. Establishment of free-flying flocks of Canada geese was very popular in east central Minnesota and western Wisconsin throughout the 1960's and early 1970's. Many of these releases were successful and now several hundred breeding pairs return to the Valley each spring.

Winter: Casual winter resident in the Western Upland, primarily associated with the St. Croix River. Nearby agricultural fields are typically used for feeding during winter.

Habitat: Canada geese are usually found nesting on semipermanently and permanently flooded wetlands in the Western Upland. Many goose nests are found on old muskrat houses in these wetlands. At Crex Meadows, nesting Canada geese typically use large man-made impoundments.

Brant (*Branta bernicla*)

Status: Accidental, three fall records.

Records: A flock of three birds clearly identifiable to this species was observed at Crex Meadows, Burnett County, on 2 October 1954 (N. R. Stone). A group of 10 brant was observed at Crex Meadows on 6 October 1974 (K. H. Dueholm). N. R. Stone observed a brant referable to the Pacific subspecies (*B. bernicla nigricans*) on 31 October 1959 at Crex Meadows. The bird was observed from 120 m; the neck markings were present and the black underwing coverts were noted, distinguishing this bird from the eastern race.

White-fronted Goose (*Anser albifrons*)

Status: Regular migrant.

Migration: Rare spring migrant, with records from Burnett, St. Croix, and Washington counties. Arrival dates do not demonstrate any pattern, ranging from 3 April 1968 and 8 April 1971 in Burnett County and 26 March 1976 in St. Croix County, to 12 April 1971 in Washington County. Most records occur during 5–20 May; the latest record was 2 June 1961 at Crex Meadows, Burnett County.

Rare fall migrant with records only from Burnett and St. Croix counties. Fall dates range from 16 September to 10 November 1964 (Crex Meadows). Most records are from 5–20 October. White-fronted geese are usually observed in fall in flocks of three to six. The largest flock recorded (12) was observed in St. Croix County on 28 March 1978.

Habitat: Spring migrants are usually observed on temporarily or semipermanently flooded wetlands. During fall migration most observations consist of birds in feeding flocks with other geese in corn or oat stubble fields.

Snow Goose (*Chen caerulescens*)

Status: Regular migrant, accidental in summer and winter.

Migration: Rare spring and fairly common fall migrant throughout the Valley; locally common at Crex Meadows, Burnett County, during fall migration. Spring migration begins with the arrival of small scattered flocks 5–15 April (earliest—16 March 1966, Washington County). No large populations occur during spring migration and most birds depart by 15 May (latest—3 June 1977, St. Croix County). Fall migrants arrive about 20 September (earliest—13 September 1974, Burnett County). Peak fall populations usually consist of groups totaling 200 to 300 individuals per county. Occasionally, exceptionally large concentrations occur at Crex Meadows Wildlife Area, including 11,650 on 2 November 1971 (WDNR files). Normal peak fall populations occur 15 October to 1 November and departure by 20 November.

Summer: N. R. Stone recorded a blue phase snow goose in molt in Black Brook Township, Polk County, on 20 June 1951. Another blue phase goose was recorded at Crex Meadows, Burnett County, on 7 July 1953.

Winter: P. D. Tweet observed a flock of six in Troy Township, St. Croix County, on 1 January 1977. These birds were probably late migrants.

Habitat: Primary habitat use of migrant snow geese consists of temporarily or semipermanently flooded wetlands. Adjacent agricultural fields, both row crops and hay, are heavily used for feeding.

Mallard (*Anas platyrhynchos*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common to locally abundant spring migrant in the Western Upland and Central Plain, fairly common to locally abundant in the Northern Highland. Determination of spring arrival dates is compounded by the presence of wintering birds. Movements of birds into the region are observed in late February with increases along the St. Croix River. Birds gradually move north arriving in the Northern Highland about 15 March. Peak spring populations occur 5–15 April; 6,000 to 8,000 birds are commonly observed in St. Croix County. Movement of nonbreeding mallards is rapid after peak periods; departure is by 1 May.

Fall migration begins 1–10 September with formation of local feeding flocks of adults and juveniles. Movements of migrants into the region begins about 20 September; peak populations occur 20 October to 1 November. Concentrations at Crex Meadows, Burnett County, have surpassed 11,000 twice (11,500 on 30 October 1967 and 15,000 on 3 November 1964). Recently, use of two refuges in St. Croix County has resulted in large numbers of mallards exceeding 10,000 (largest, 13,500 on 20 October 1977). Movement from the region is dependent on weather conditions. Departure of the largest number of birds occurs by 20 November and those not wintering have departed by 15 December.

Nesting Season Distribution: Common breeding duck throughout the region; nesting has been reported from all counties. Most research has centered on breeding populations in the pothole region of St. Croix and southern Polk counties, and at Crex Meadows. In the former area, Peterson (1978) estimated a breeding population of mallards of nearly 1.4 pairs per km^2. At Crex Meadows, the estimated number of mallard breeding pairs on waterfowl survey transects ranged from 7 in 1973 to 55 in 1977 (WDNR files).

Winter: Common wintering duck wherever open water is available. Large early winter flocks are usually associated with open water areas along the St. Croix River. Cooper and Johnson (1977) reported that 75 to 200 mallards wintered near Afton, Washington County, from 1974 to 1977. Substantial wintering populations are also known to occur along the Kinnickinnic River in Pierce County and southern St. Croix County.

Habitat: Nesting mallards occupy a variety of wetland classes ranging from sedge meadows and acidic bogs to permanently flooded wetlands. Nesting pairs also use lowland forest habitat along rivers and streams, man-made impoundments, and stock-watering ponds created by the Soil Conservation Service. With the almost complete destruction of native grassland habitat, these ducks now commonly nest in haylands and oat and corn fields. Several thousand acres of Managed Grasslands have been established by government agencies to provide dense waterfowl nesting cover.

Black Duck (*Anas rubripes*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Uncommon spring migrant in all regions; fairly common in the fall in the Northern Highland and locally at the Crex Meadows Wildlife Area, Burnett County. Spring migrants arrive along the St. Croix River about 15 March, generally moving to natural basin wetlands 1–10 April. No peak spring concentrations of black ducks have been noted, although they are most frequently observed 10–25 April. Departure from nonbreeding areas usually occurs by 15 May. Stragglers have been noted during late May and throughout the summer, primarily in the Western Upland.

Fall migrants arrive in the Western Upland 5–10 September. Peak fall populations occur 20 October to 10 November. Largest concentrations have been noted at the Crex Meadows Wildlife Area, Burnett County; 1,000 individuals were recorded 14 November 1964, 7 November 1965, and 28 October 1966. In the Western Upland, greatest numbers occur in central St. Croix County and along the St. Croix River and backwaters 25 October to 5 November. During fall migration, black ducks are usually observed in close association with flocks of mallards. Departure during fall occurs 15 November to 1 December, depending on weather conditions.

Nesting Season Distribution: Locally occurring nesting duck, primarily in the Northern Highland. Green and Janssen (1975) have mapped the breeding distribution of this duck in Minnesota and indicated it as a regular nesting bird in northern Pine County. There are two Washington County nest records: 24 May 1971, a female with 10 young was observed near Hugo, Minnesota, and nesting was reported during the summer of 1978 (Green 1979). Pair counts at Crex Meadows from 1957 to 1976 revealed an average of 1.1 pairs per year; broods were observed in 1957 and 1971 (WDNR files). Jackson (1941) observed one black duck near Solon Springs, Douglas County, on 8 August 1919. In St. Croix County, one pair was observed near New Richmond on 28 June 1975. They may have been nonbreeding birds or late migrants.

Winter: Fairly common winter resident wherever there is open water. Recorded primarily along the lower St. Croix River (Hudson-Stillwater) and below the dam at Taylors Falls. One midwinter record for Crex Meadows, Burnett County, 12 January 1955.

Habitat: The black duck is primarily a species of northern forested wetlands. Typical habitat consists of 0.5 ha or larger permanently flooded wetlands that are slightly acidic. Pairs and broods have also been noted on acid bog wetlands and beaver ponds.

Gadwall (*Anas strepera*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Uncommon migrant in the Western Upland and Central Plain; uncommon to rare in the Northern Highland except at Crex Meadows. Spring migrants arrive 25 March to 5 April in the Western Upland, reaching the Northern Highland 10–15 April (earliest—31 March 1958, Burnett County). Peak spring migration occurs 15–25 April and departure of nonbreeders occurs 5–15 May.

Fall migrants arrive 20–30 September reaching peak numbers 10–15 October. The largest concentration recorded at Crex Meadows, Burnett County, was 400 on 3 October 1970, and the largest number on the St. Croix County wetlands was 150 on 10 October 1975. Departure of fall migrants occurs after mid-October and most birds have left by 10 November.

Nesting Season Distribution: Rare and local nesting species with confirmed brood records from St. Croix, Polk, and Burnett counties. Gadwalls were released at the Crex Meadows Wildlife Area, Burnett County, during 1970 in an attempt to establish this prairie duck on seeded native prairie grasslands.

This release met with limited success because the first brood was not observed until 1974. In the prairie wetlands of southern Polk and central St. Croix counties, gadwalls occur as a rare nesting species in a narrow band between Roberts (St. Croix County) and Alden Township (Polk County).

Winter: One bird was recorded on the Afton CBC in St. Croix County on 1 January 1973.

Habitat: Nesting gadwalls at Crex Meadows are generally associated with man-made potholes constructed to resemble natural basin wetlands. In St. Croix and southern Polk counties, breeding pairs are typically associated with seasonally and semipermanently flooded wetlands. Vegetation of these wetlands is composed of cattail, bulrushes, and various other emergent species.

Pintail (*Anas acuta*)

Status: Regular migrant and nesting species, one winter record.

Migration: Fairly common spring migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Pintails are among the first dabbling ducks to arrive in the region, usually 5–15 March. Peak spring populations occur 10–20 April, and depart by 15 May. Goddard (1975) found that pintails made up 0.9% of the spring migrant waterfowl in St. Croix County and 2.8% of the migrant dabbling duck population.

Fall migrants arrive in late August. During the fall, pintails are fairly common at Crex Meadows, Burnett County, in central St. Croix, and eastern Washington counties, and in southern Polk County. They are rare and local in other regions during this period. Peak fall populations occur 25 September to 10 October and departure occurs by 15 November. Largest fall populations at Crex Meadows have been 400 birds reported on 4 October 1956, 29 September 1964, and 27 September 1973.

Nesting Season Distribution: Uncommon and local nesting species with records from Washington (Green and Janssen 1975), St. Croix, Polk, and Burnett counties. In central St. Croix and southern Polk counties, pintails made up 0.8% of the breeding duck population (Peterson 1978). At Crex Meadows, waterfowl pair counts indicated that pintails constituted about 1% of the yearly breeding population from 1957–78 (WDNR files).

Winter: One pintail was observed on the St. Croix River, Burnett County, on 12 and 13 January 1949 (Robbins 1949). Afton CBC data include single pintails on 1 January 1972 and 1973, and two birds on 1 January 1974, 1976, and 1978.

Habitat: Nesting pintails are typically associated with seasonally and semipermanently flooded wetlands that support a lush growth of emergent aquatic vegetation.

Green-winged Teal (*Anas crecca*)

Status: Regular migrant and nesting species, two winter records.

Migration: Fairly common migrant in all regions, locally common during spring in the Western Upland. Spring migrants begin to arrive in the Western Upland 25 March to 1 April (earliest—15 March, St. Croix County). Arrival in the Northern Highland occurs 5–10 April. Peak spring populations occur 15–25 April and departure of nonbreeding birds occurs by 15 May. In St. Croix County, Goddard (1975) found that green-winged teal made up 4.6% of the spring waterfowl population and 13.6% of the dabbling ducks.

Fall migration begins about 25 August with a slow increase of numbers in the Central Plain and Northern Highland. Peak populations occur 1–15 October in the Northern Highland. The largest population recorded at Crex Meadows, Burnett County, was 600 birds on 2 October 1971. Peak fall populations in the Western Upland occur 10–25 October. Although departure is fairly slow, most green-winged teal have departed by 15 November.

Nesting Season Distribution: Uncommon to rare nesting species throughout the Valley. Most observations of birds during this period are made in the prairie wetland region of St. Croix, Polk, and Washington counties, and at Crex Meadows. Green-winged teal are the fourth most common breeding duck at Crex Meadows (WDNR files). In St. Croix and Polk counties, green-winged teal constitute about 0.4% of the breeding waterfowl population.

Winter: One bird was observed on the Afton CBC on 1 January 1972. N. R. Stone observed three birds at Clam Lake, Burnett County, on 13 February 1950 (Robbins 1950*a*).

Habitat: Pairs and broods are associated with seasonally and semipermanently flooded wetlands. Of seven green-winged teal nests that I located in St. Croix County in 1976, all were in alfalfa fields.

Blue-winged Teal (*Anas discors*)

Status: Regular migrant and nesting species.

Migration: Abundant migrant in the Western Upland, common in the Central Plain, and fairly common (locally common) in the Northern Highland. Goddard (1975) found that blue-winged teal made up 14.4% of all waterfowl and 43% of all dabbling ducks using St. Croix County wetlands in spring.

Blue-winged teal are among the last migrant ducks to arrive in spring; average arrival date is 5 April (earliest—23 March 1976, St. Croix County). Populations build rapidly and peak numbers are usually noted 20 April to 10 May. The first migrants usually arrive in the Northern Highlands about 20 April and reach peak populations 5–15 May.

Fall migrants begin to form large feeding aggregations in late July and early August. Peak fall populations occur early; the largest number (1,200) observed at Crex Meadows, Burnett County, was on 17 September 1976. Typically, large numbers of blue-winged teal are observed 10–25 September in St. Croix and Washington counties (1,000 on 23 September 1975). Departure from the region is very rapid after peak populations occur, and most birds are gone by 20 October (latest—2 December 1973, Washington County).

Nesting Season Distribution: Abundant nesting duck on prairie wetlands of St. Croix, Polk, and Washington counties. Preliminary data collected by the WDNR (Peterson 1978) show a breeding density of about 1.7 pairs per km^2 in St. Croix and Polk counties. At Crex Meadows, blue-winged teal are the most abundant breeding duck, averaging nearly 42% of all breeding pairs observed from 1957–78 (WDNR files).

Habitat: Blue-winged teal use a wide variety of wetland types for nesting, ranging from sedge meadows to bog wetlands. Largest densities occur on seasonally, semipermanently, and permanently flooded wetlands containing an abundance of submerged and emergent aquatic vegetation. To a lesser extent, breeding pairs also use stock ponds and dugout ponds created by the Soil Conservation Service. Lowland Deciduous Forest habitat along streams and rivers is regularly used.

Cinnamon Teal (*Anas cyanoptera*)

Status: Casual spring and fall migrant.

Records: Cinnamon teal have been observed four times at Crex Meadows, Burnett County: 14 April 1953 (six birds); 25 April 1955 (two); 8 May 1956. Hunt and Jahn (1968) observed a male cinnamon teal at Crex Meadows on 21 April 1968. One bird was observed in Washington County on 16 April 1963 (Honetschlager 1963). Roberts (1932) cited the collection of a male cinnamon teal near Stacy, Chisago County, "sometime between October 5-15, 1923." A second male was obtained "at almost identically the same place" on 15 September 1924.

American Wigeon (*Anas americana*)

Status: Regular migrant and casual nesting species.

Migration: Fairly common migrant in the Western Upland; uncommon in the Central Plain and Northern Highland. Goddard (1975) found that American wigeon made up 2.2% of all waterfowl and 4.5% of the dabbling ducks using St. Croix County wetlands during spring migration.

Spring migrants arrive in the Western Upland 20–30 March; the earliest birds occur along the St. Croix River. Arrival is somewhat later at Crex Meadows, Burnett County, where the average arrival is 8 April. Movement into the Valley is very rapid and peak populations are usually observed 10–25 April. Departure from the Valley usually occurs 10–25 May.

Fall migrants arrive in late August and build up rapidly, reaching peak populations 25 September to 10 October. The largest number observed at Crex Meadows (400) occurred on 3 October 1970. In St. Croix County, fall peak populations of 200 to 300 birds are common and 720 were observed on 3 October 1976. Departure from the Valley occurs 1–10 November (latest—15 December 1974, Washington County).

Nesting Season Distribution: Nest records of American wigeon have been confirmed only at Crex Meadows: two broods (eight each) in July 1967 (first brood observed on 14 July); one brood observed in 1970 and 1971; one brood of four observed on 21 July 1975, and two broods during 1976. Elsewhere, summering pairs are regularly observed in St. Croix and Polk counties. The only evidence suggestive of nesting was a female acting "broody" on a pond 1.6 km northwest of New Richmond on 20 July 1977. Although summering pairs are regularly observed in Washington County near Lake Elmo, no evidence of nesting has been obtained.

Habitat: Breeding pairs at Crex Meadows are typically associated with large man-made impoundments. In St. Croix and Washington counties summering American wigeon pairs are associated with semipermanently flooded wetlands.

Northern Shoveler (*Anas clypeata*)

Status: Regular migrant and nesting species.

Migration: Fairly common spring migrant in the Western Upland, uncommon to rare elsewhere. Rare throughout the Valley during fall migration. Goddard (1975) found that the northern shoveler made up 2.2% of the waterfowl population and 6.4% of the dabbling duck population in St. Croix County during spring migration.

Spring migrants arrive 1–5 April (earliest—24 March 1976, St. Croix County). Peak spring migration in the Western Upland occurs 20 April to 5 May and departure occurs 15–20 May. Elsewhere, arrival occurs 10–20 April (average 15 April at Crex Meadows). Peak spring populations occur about 10 May and departure by 20 May. Fall migrants begin to arrive 10–20 August. Peak fall populations cannot be determined because of the small number of birds usually observed. Departure from the Valley occurs by 15 November.

Nesting Season Distribution: Regular nesting species at Crex Meadows, Burnett County, where up to eight pairs per year have been recorded on breeding waterfowl survey transects (WDNR files). Elsewhere, northern shovelers are encountered irregularly during the breeding season in St. Croix, southern Polk, and Washington counties.

Habitat: Soft-bottomed semipermanently and permanently flooded wetlands supporting populations of macroinvertebrates are usually occupied during the nesting season. During spring migration, extensive use is made of temporarily flooded wetlands.

Wood Duck (*Aix sponsa*)

Status: Regular migrant and nesting species, casual in early winter.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–20 March (earliest—6 March 1975, Pierce County). Spring migration progresses according to the opening of river systems and arrival in the Northern Highland occurs 1–10 April. Peak spring migration occurs 15–25 April in the Western Upland and 25 April to 5 May in the Northern Highland. Goddard (1975) reported that wood ducks constituted 0.4% of the total spring waterfowl population and 1.2% of the dabbling duck population on prairie wetlands in St. Croix County. This low percentage is undoubtedly related to their preference for riverine habitats.

Fall migration begins during mid-August with the formation of feeding groups. A gradual buildup in numbers occurs throughout September. Peak populations at Crex Meadows, Burnett County, usually occur 20 September to 5 October; the largest groups were noted on 4 October 1967 (1,500) and 14 September 1968 (1,000). Elsewhere, peak populations occur 1–20 October. Especially important riverine staging areas occur along the Kettle River (Pine County), Apple River (Polk and St. Croix counties), and Willow River (St. Croix County). Departure from the Valley occurs rapidly after mid-October; the latest dates were 20 November 1976 and 20 December 1956 (both Washington County).

Nesting Season Distribution: Uncommon to fairly common nesting species in all regions. Nesting records exist for all counties and nesting birds are numerous along the larger tributaries of the St. Croix River. In St. Croix County, the wood duck ranks third in abundance behind mallard and blue-winged teal as a breeding duck (B. A. Moss, personal communication).

Winter: Winter records include 1 January 1972 and 1973 (Afton CBC, Washington County); 27 December 1970 (Solon Springs CBC, Douglas County); and 20 January 1975 (McKenzie Creek, Polk County).

Habitat: Primary habitat use by nesting wood ducks includes wooded streams, rivers, backwater sloughs, and wooded lakes. In the Northern Highland, breeding pairs also use tamarack bogs and spruce-lined lakes. In the Western Upland, use of prairie wetlands has been enhanced by the placement of artificial nest boxes.

Redhead (*Aythya americana*)

Status: Regular migrant and casual nesting species.

Migration: Fairly common migrant in the Western Upland, particularly in western St. Croix and eastern Washington counties. Uncommon to rare elsewhere, especially in the Northern Highland. Spring migrants arrive in the Western Upland 5–10 April (earliest—23 March, St. Croix County). Peak abundance occurs 25 April to 5 May and most have departed by 25 May. Goddard (1975) found that redheads made up 2% of the total spring waterfowl population and 4.5% of the spring diving duck population in St. Croix County. At the Crex Meadows Wildlife Area, Burnett County, the average date of spring arrival is 15 April; peak populations occur 1–10 May, and departure by 1 June.

Fall migrants begin to arrive 10–20 September. Populations build slowly through October, reaching largest numbers 20 October to 1 November. The principal fall migration route used by redheads is south of the Valley. Because of this, concentrations larger than 50 birds are rarely encountered during fall migration. Departure from the region occurs rapidly after 15 November; occasional stragglers linger along open areas of the St. Croix River until 1 December.

Nesting Season Distribution: There are six breeding records for the Valley: a female with a brood of four on West Twin Lake, St. Croix County, 1968 (J. T. Lokemoen); a female with a brood of four on East Twin Lake, St. Croix County, 1975 (B. A. Moss); females with broods of five and six on the Gust Waterfowl Production Area, St. Croix County, 1976 and 1977 (C. A. Faanes); two broods of six and seven on Oakridge Lake during July 1976. Elsewhere, occasional summering pairs have been observed in central Washington and southern Polk counties, although no broods have been observed. At Crex Meadows, summering pairs are noted almost yearly, although the only suggestion of nesting was a female acting "broody" on 16 June 1975 (S. D. Robbins, personal communication).

Habitat: All redhead broods have been observed on large permanently flooded wetlands where the dominant emergent vegetation consists of cattail and river bulrush.

Ring-necked Duck (*Aythya collaris*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Abundant migrant throughout the Valley. Spring migrants arrive in the Western Upland about 15 March and the Northern Highland 1–5 April (earliest—20 March 1950, Burnett County). Peak populations of spring migrants occur 20 April to 1 May. Goddard (1975) found that ring-necked ducks were the second most abundant spring migrant duck in St. Croix County, making up 14.8% of the total waterfowl population and 32.8% of the diving duck population. Departure from nonbreeding areas occurs by 20 May.

Fall migrants begin to form flocks in the Northern Highland in mid-September and the first migrants reach the Western Upland about 25 September. Peak fall populations at Crex Meadows, Burnett County, usually occur 20–30 October and have included 5,000 (25 October 1967), 5,500 (25 October 1965), and 7,500 (26 October 1966). In the Western Upland, peak populations occur about 1 November and include up to 1,500 birds (B. A. Moss, personal communication). Departure from the Valley occurs steadily through November with stragglers occurring along the St. Croix River until 1 December.

Nesting Season Distribution: Uncommon nesting species in the Western Upland; fairly common in the Central Plain and Northern Highland, common at Crex Meadows. Breeding records have been obtained in all counties except Pierce and the breeding range includes the area north of Marine-on-St. Croix and New Richmond.

Breeding waterfowl surveys at Crex Meadows reveal that the ring-necked duck is the third most numerous nesting species (WDNR files). In St. Croix and southern Polk counties, Peterson (1978) found that ring-necked ducks constituted an insignificant percentage of the breeding population. However, most ring-necked duck breeding activity in St. Croix and Polk counties occurs west and north of Peterson's study area.

Winter: One male was observed on the Afton CBC 1 January 1975.

Habitat: Ring-necked ducks are primarily a species of permanently flooded wetlands in the forested areas of the Valley. Typical brood habitat consists of slightly acidic water and scattered growths of pond lily, bulrush, and cattail. Beaver ponds are commonly used in the northern counties and acid bogs are occasionally used.

Canvasback (*Aythya valisineria*)

Status: Regular migrant and casual summer resident, one nesting record and one winter record.

Migration: Uncommon spring and fall migrant in the Western Upland and Central Plain, rare in the Northern Highland. Spring migrants arrive in late March (earliest—16 March). Peak abundance occurs 10–25 April and departure occurs 10–20 May .Goddard (1975) found that the canvasback made up 0.4% of the total spring waterfowl population and 1.0% of the diving duck population in St. Croix County. Fall migration begins in mid-September with arrival of small flocks on the larger lakes and the St. Croix River. Peak fall populations occur 15 October to 1 November and departure by 30 November.

Nesting Season Distribution: Casual summer resident in St. Croix County and at Crex Meadows, Burnett County. The only nesting record is my observation of a hen with a brood of eight on Oakridge Lake, St. Croix County, on 8 July 1976. Summering pairs are occasionally observed on other prairie wetlands although no evidence of nesting is available. Elsewhere, summering pairs were observed at Crex Meadows in 1950, 1962, 1975, and 1978.

Winter: A male canvasback was observed on the Afton CBC, Washington County, on 1 January 1975.

Habitat: The nesting record was obtained on a large permanently flooded wetland. Dominant vegetation included softstem bulrush, cattail, and river bulrush. Most additional summer records are the birds on semi-open permanent wetlands. During migration, canvasbacks utilize most wetland types, although a preference is shown for semipermanently and permanently flooded wetlands.

Greater Scaup (*Aythya marila*)

Status: Regular migrant.

Migration: Rare migrant throughout the Valley. Spring migrants arrive 5–15 April and are most regularly observed 25 April to 5 May. First migrants are usually observed on the St. Croix River, followed by an increase of observations away from the river. Departure from the Valley occurs by 15 May (latest—29 May 1968, Burnett County). Goddard (1975) failed to record the greater scaup during four spring field seasons in St.

Croix County.

Fall migrants occur 5 October to 20 November; most records are 20 October to 5 November. Fall migrants are usually observed intermixed with large rafts of lesser scaup, whereas in spring migration, greater scaup seem to be more segregated from lesser scaup.

Habitat: Large, open permanently flooded wetlands typically support the most greater scaup in this region. Cedar Lake on the Polk-St. Croix County line is probably the most productive lake in the region for observing greater scaup.

Lesser Scaup (*Aythya affinis*)

Status: Regular migrant, casual nesting species, and occasional in early winter.

Migration: Abundant migrant throughout the Valley. The lesser scaup is the most numerous migrant duck in the Valley. In St. Croix County, Goddard (1975) found that lesser scaup made up 24.6% of the total spring waterfowl population and 54.6% of the diving duck population. Spring migrants arrive in the Western Upland 10-15 March (earliest—6 March 1976, Washington County) and the Northern Highland 1-10 April. Peak spring populations occur 20 April to 10 May when flocks of 700 to 1,000 individuals are typically observed on larger lakes. Departure occurs 20-30 May.

Fall migrants arrive 20 September to 1 October. Fall migration is characterized by a rather low increase in numbers until about 20 October when large influxes occur. Peak fall populations at Crex Meadows Wildlife Area, Burnett County, occur 25 October to 5 November and have totaled up to 7,000 individuals (30 October 1965). In the Western Upland, peak fall populations larger than 3,000 individuals are observed 25 October to 5 November. Departure from the Valley is dependent on ice conditions on larger lakes; most birds depart by 1 December.

Nesting Season Distribution: Regular summer resident on wetlands in Polk, St. Croix, and central Washington counties. Usually up to 10 pairs can be found on wetlands near New Richmond, St. Croix County. There are two brood records for the Valley; both broods were found on 7 July 1976, on wetlands in Alden Township, Polk County. These broods were within 0.8 km of each other and constituted the eighth and ninth, 20th century breeding records for Wisconsin. At Crex Meadows, 10 pairs were observed during 1958. Since then at least one pair has been present yearly; however, no broods have been observed. Jackson (1942) reported the collection of a male lesser scaup on Upper St. Croix Lake, Douglas County, on 1 August 1919.

Winter: Occasional early winter visitor primarily on open stretches of rivers. These birds are probably late fall migrants rather than wintering birds because no midwinter records exist. Dates range from 22 December 1956 to 1 January 1973, 1975, 1976 (Afton CBC); 29 December 1973 to 3 January 1976 (Suburban St. Paul CBC); 12-13 January 1949, 12 January 1955, 9 January 1956, and 7 January 1957 (Crex Meadows); 31 January 1949, St. Croix Falls (Polk County); and 23 December 1975, Solon Springs CBC

(Douglas County).

Habitat: The Polk County broods were observed on semipermanently flooded wetlands. Dominant vegetation included cattail, burreed, and coontail. Most summering pairs are observed on small semipermanent wetlands.

Common Goldeneye (*Bucephala clangula*)

Status: Regular migrant and winter resident, one summer record.

Migration: Common migrant throughout the Valley, most numerous along the St. Croix River and on large lakes of the Northern Highland. Fall migrants arrive in the Northern Highland 20 September to 1 October and reach the Western Upland 10–20 October. Peak fall common goldeneye populations occur 10–30 November.

Spring migrants reach peak abundance 10 March to 1 April and most have departed by 1 May (latest—30 May 1967, Burnett County). Movement of spring migrants is similar to fall; most birds use rivers and large lakes. Goddard (1975) found that common goldeneyes on prairie wetlands made up $<1\%$ of the total spring waterfowl population; his 4-year observations totaled 707 individuals. On the St. Croix River <16 km from Goddard's study area, daily totals in excess of 100 individuals were recorded on 8 March 1975, 11 March 1977, and 9 April 1978. Yearly totals in excess of 2,000 individuals along the St. Croix River were regularly recorded from 1972 to 1978.

Winter: Common winter resident wherever open water is present. Primary wintering populations occur at the confluence of the St. Croix and Mississippi Rivers at Prescott, Wisconsin (150 to 200 individuals); below the Alan S. King generating plant at Bayport (Washington County); near Hudson (425 on 1974 Afton CBC and 360 on 1975 Afton CBC); and below the electric generating dam at St. Croix Falls–Taylors Falls (50 to 100 individuals).

Summer: S. D. Robbins observed a lone male throughout the summer of 1967 in St. Croix County.

Habitat: Large open stretches of rivers that apparently support healthy populations of fishes and invertebrates. During migration, common goldeneyes are typically associated with large (>20 ha) permanent lakes.

Barrow's Goldeneye (*Bucephala islandica*)

Status: Accidental, two records.

Records: Faanes and Goddard (1976) cited one observation from East Twin Lake, St. Croix County, on 8 May 1975. M. R. Olson observed one male along Trout Brook Road near Hudson, St. Croix County, on 1 January 1977. The bird was observed again on 2 January 1977 on the St. Croix River.

Bufflehead (*Bucephala albeola*)

Status: Regular migrant, one summer and one winter record.

Migration: Fairly common migrant in the Western Upland and Central Plain; common on forested lakes in the Northern Highland. Goddard (1975) found that buffleheads constituted 1.6% of the total spring waterfowl population and 3.5% of the diving duck population on prairie wetlands in central St. Croix County.

Spring migrants arrive in the Western Upland 20 March to 1 April (earliest—13 March 1966, Washington County) and peak populations occur about 20 April. Migrants arrive in the Northern Highland 1–10 April, reaching peak numbers 15–25 April. Departure from the Valley occurs by 25 May. Fall migrants arrive in the Northern Highland about 1 October and the Western Upland about 5 October. Peak fall populations occur 20 October to 1 November and departure occurs by 25 November. Peak fall populations on central St. Croix County wetlands usually total 150 to 200 individuals.

Summer: S. D. Robbins observed a lone bufflehead at Crex Meadows, Burnett County, on 17 June 1976. This may have been an injured bird.

Winter: A flock of 40 buffleheads was observed on the St. Croix River near Grantsburg, Burnett County, from 12–13 January 1949 (Robbins 1949).

Habitat: Buffleheads are associated with a variety of wetland types during spring migration, including temporarily, seasonally, and permanently flooded wetlands, and riverine habitats. During fall migration buffleheads are usually associated with large semipermanently and permanently flooded wetlands.

Oldsquaw (*Clangula hyemalis*)

Status: Casual, five records.

Records: Oldsquaw were observed on Oakridge Lake near New Richmond, St. Croix County, on 24 October 1974 (S. R. Schneider); 14 October 1975 (R. E. Faanes); and 2 October 1977 (C. A. Faanes). One was observed at Crex Meadows Wildlife Area, Burnett County, on 22 April 1952 (Strelitzer 1952). In Washington County, three birds were observed on 6 January 1965.

Common Eider (*Somateria mollissima*)

Status: Accidental, one record.

Record: One female common eider was shot on Phantom Lake, Crex Meadows Wildlife Area, Burnett County, on 10 November 1968 (Tessen 1969*b*).

White-winged Scoter (*Melanitta deglandi*)

Status: Casual, four records.

Records: N. R. Stone observed one at Crex Meadows, Burnett County, on 8 May 1950 (Robbins 1950*b*), and R. Brown observed one there on 12 August 1975. C. A. Faanes and W. Norling observed a female on Oakridge

Lake, St. Croix County, on 18 October 1974. I observed a female at Amery, Polk County, on 9 November 1976.

Surf Scoter (*Melanitta perspicillata*)

Status: Casual, three records.

Records: A single surf scoter was observed at Crex Meadows Wildlife Area, Burnett County, on 5 October 1974. On 6 October 1974, two birds were shot from a group of four at Crex Meadows by J. O. Evrard. Photos were taken of the two birds. B. A. Moss observed a flock of six surf scoters on Deer Lake, Polk County, on 30 October 1975.

Black Scoter (*Melanitta nigra*)

Status: Casual, two records.

Records: A female black scoter was observed on West Twin Lake near Roberts, St. Croix County, on 18 October 1974 (Faanes and Goddard 1976). On 1 January 1977, I observed a female black scoter with a group of black ducks and mallards at the mouth of the Kinnickinnic River, Pierce County (Lien and Lien 1977).

Ruddy Duck (*Oxyura jamaicensis*)

Status: Regular migrant and nesting species, accidental in winter.

Migration: Fairly common migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Goddard (1975) reported that ruddy ducks constituted 1% of the total spring waterfowl population and 2.2% of the diving duck population in St. Croix County. Ruddy ducks are the latest arriving waterfowl species in spring. The average arrival date is 10 April in St. Croix County and 25 April at Crex Meadows, Burnett County (earliest dates—24 March 1976, St. Croix County and 4 April 1948, Burnett County). Peak spring populations in St. Croix, Polk, and Washington counties occur 25 April to 10 May; departure of nonbreeding birds is by 20 May. Fall migration begins in early September and peak numbers occur 25 September to 15 October. The largest groups recorded during fall migration range from 25 to 30 birds per wetland. Departure from this region occurs by 1 November (latest—27 November 1967, Washington County).

Nesting Season Distribution: Uncommon and local breeding duck on prairie wetlands of St. Croix, Polk, and Washington counties. These breeding populations occur in pockets of high density wetlands in the respective counties. Peterson (1978) reported that ruddy ducks made up $<1\%$ of the total breeding duck population in St. Croix and Polk counties. Three brood records have been obtained at Crex Meadows, two in 1973 and one in 1974.

Winter: One ruddy duck was observed on the Afton CBC on 22 December 1956.

Habitat: Ruddy ducks are characteristic of semipermanently and permanently flooded wetlands that are dominated by cattail, hardstem bulrush, and river bulrush. Most wetlands occupied by breeding ruddy ducks vary from 1-3 m deep.

Hooded Merganser (*Lophodytes cucullatus*)

Status: Regular migrant and nesting species, two winter records.

Migration: Uncommon migrant throughout the Valley, fairly common locally along heavily wooded lakes and streams in the Northern Highland. Goddard (1972) reported that hooded mergansers made up 0.2% of the total spring waterfowl population in St. Croix County. This low percentage resulted from censusing prairie wetlands that are not utilized regularly by hooded mergansers. Spring migrants arrive in the Western Upland 1–10 April (earliest—23 March 1968, St. Croix County) and the Northern Highland about 10 April (earliest—14 March 1966, Burnett County). Peak abundance occurs 20 April to 5 May and departure from nonbreeding areas occurs by 15 May. Fall migration begins in early September in the Northern Highland and migrants reach the Western Upland about 15 September. Peak fall populations occur 15 October to 1 November and departure by 20 November. Peak fall populations in western Wisconsin range from 50 to 75 birds on important staging wetlands.

Nesting Season Distribution: Fairly common (and local) breeding duck throughout the Valley. Hooded mergansers make up a small proportion of the breeding population on prairie wetlands where the most intensive surveys have been conducted. Lack of survey work along streams and in wooded lake regions contributes to the poor understanding of their breeding distribution.

Winter: There are two winter records including one bird along the St. Croix River near Grantsburg, Burnett County, on 9 January 1956 and one bird on the Afton CBC on 1 January 1975.

Habitat: In the Western Upland and Central Plain, breeding hooded mergansers use heavily wooded river and stream habitats for breeding. An abundance of dead trees providing natural nesting cavities is an important component of their breeding habitat. In the Northern Highland, breeding birds occupy large forest-bordered lakes and acidic bog-type lakes in addition to riverine habitats.

Common Merganser (*Mergus merganser*)

Status: Regular migrant and winter resident, two summer records.

Migration: Common migrant throughout the Valley. Goddard (1975) reported that common mergansers made up 0.1% of the total spring waterfowl population in St. Croix County. This estimate reflects late dates of censusing, which did not coincide with the peak migration period of this bird, rather than an actual low population. Spring migration begins with a noticeable influx about 20 February. Spring populations build rapidly through March reaching peak numbers 20–30 March and most birds have departed by 30 April. Fall migrants arrive in the Northern Highland 20–30 September and reach the Western Upland about 10 October. Peak fall populations occur 10 November to 1 December and nonwintering birds have departed by 15 December. During peak fall periods, up to 1,000 individuals have been recorded along the lower St. Croix River in Washington County.

Winter: Uncommon winter resident of the lower St. Croix River and along open stretches of water on major tributaries. The largest group recorded on the Afton CBC was 65 birds on 1 January 1958. Winter populations are directly related to the severity of winter weather. During 1974–75, groups of 30 to 35 common mergansers were regularly observed along the St. Croix River through late December and early January. The record cold of 11 January 1975 (–40 °C), froze nearly the entire river system and common mergansers were not observed again until mid-February when the first migrants returned.

Summer: Three common mergansers were observed in Chisago County on 16 June 1975 (Eckert 1976), and a lone male was observed near New Richmond, St. Croix County, on 27 June 1975. These birds undoubtedly were lingering migrants.

Habitat: Primarily a species of large, deep, permanently flooded wetlands and the major rivers of the Valley.

Red-breasted Merganser (*Mergus serrator*)

Status: Regular migrant, two summer and one winter records.

Migration: Fairly common migrant throughout the Valley, occasionally common on larger lakes of the Central Plain. Goddard (1975) reported that red-breasted mergansers made up only 0.3% of the total spring waterfowl population in St. Croix County. This estimate indicates that censuses were concentrated on smaller wetlands and were not conducted to coincide with peak migration.

Spring migrants arrive in the Western Upland about 20 March and reach the Northern Highland 1–10 April. Peak spring migration occurs 10–25 April and departure by 15 May. Fall migrants arrive in the Northern Highland 20–30 September and reach the Western Upland about 10 October. Peak fall populations occur 25 October to 15 November and departure by 10 December. During the peak of fall migration, concentrations of 50 to 75 birds are typically recorded on important staging wetlands.

Summer: A lone female was observed at Crex Meadows, Burnett County, on 1 July 1955. In Washington County an injured bird was observed 24 June 1975 (Eckert 1976).

Winter: A group of four was observed on the St. Croix River on the Afton CBC, 1 January 1975. Five were observed in St. Croix County on 5 January 1942 (Barger 1942).

Habitat: Red-breasted mergansers are characteristic of large, deep-water permanently flooded wetlands and riverine habitats. Occasional small groups of migrants occur on semipermanently flooded wetlands during spring migration.

FAMILY CATHARTIDAE: American Vultures

Turkey Vulture (*Cathartes aura*)

Status: Regular migrant and probable nesting species.

Migration: Fairly common migrant throughout the Valley, becoming common at Crex Meadows during the fall. Spring migrants arrive during the first week of April (earliest—24 March 1963 and 1977, Pierce County). Peak spring migration occurs between 20 April and 1 May and most depart by 15 May. Peak fall migration occurs 15–25 September; departure occurs by 15 October (latest—23 November 1948 and 30 November 1950, Burnett County).

Nesting Season Distribution: Rare to uncommon summer resident throughout the Valley, most regularly observed in the forested regions along the upper St. Croix River. Roberts (1932) reported turkey vultures nesting "along the St. Croix River"; however, he provided no dates or locations. Turkey vultures are regularly observed during the summer between Prescott and Stillwater. This area of extensively wooded bluffs provides excellent breeding habitat for vultures. Although young are observed during late July, no nests have been found.

Habitat: Habitat used by turkey vulture during the nesting season consists of Southern Deciduous Forest occurring on bluffs along the St. Croix River.

FAMILY ACCIPITRIDAE: Hawks and Harriers

Swallow-tailed Kite (*Elanoides forficatus*)

Status: Accidental, one record.

Record: One bird was found dead along Highway 95 near Marine-on-St. Croix, Washington County, on 29 April 1966. The specimen is now in the collection of the Minnesota Museum of Natural History (#23152).

Mississippi Kite (*Ictinia mississippiensis*)

Status: Accidental, one record.

Record: A single bird was observed at Crex Meadows, Burnett County, on 27 May 1976 (Hofslund and Niemi 1977).

Northern Goshawk (*Accipiter gentilis*)

Status: Regular migrant and winter resident, casual nesting species.

Migration: Rare migrant throughout the Valley. Most regularly observed in the forested areas of the Northern Highland and Central Plain, casual in the Western Upland. Fall migrants begin to arrive in mid-September and are most conspicuous from mid-October to mid-December. Spring migration begins in late February with dispersal toward nesting areas. Goshawks are most conspicuous in spring 15 March to 10 April and have departed by 30 April.

Nesting Season Distribution: One nesting record for Burnett County; an adult incubating during May 1973 (W. Norling). A nest at Camp Wilder, Washington County, in 1967, was abandoned because of excessive human activity in the immediate area (Huber 1967). Numerous sight records, primarily from the Northern Highland, indicate that additional nesting records are probable.

Winter: Rare to uncommon winter resident throughout the Valley. Most frequently observed in the heavily forested Northern Highland.

Habitat: The Burnett County nest was in mixed jack pine–oak habitat. Additional nesting season records have been obtained from mature Northern Hardwood Forest, mixed coniferous forest, and jack pine–oak habitat.

Sharp-shinned Hawk (*Accipiter striatus*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Uncommon spring and fairly common fall migrant throughout the Valley. Occasionally 30 to 40 migrant sharp-shinned hawks can be observed per day along the St. Croix River. Spring migration begins in mid-March; largest numbers occur 10–25 April. Most birds have arrived on nesting territories by 10 May. Fall migration begins in mid-August and peak numbers are reached 10 September to 10 October. Most have departed by 15 November.

Nesting Season Distribution: Uncommon to rare during the nesting season in the Central Plain and Northern Highland. Although this hawk is regularly observed during the nesting season, only one nest has been found. On 23 May 1976, I found one sharp-shinned hawk nest in the McKenzie Creek Wildlife Area, Polk County. Other observers, primarily Jackson (1941) and Bernard (1967) have recorded this species during the nesting season but failed to find a nest. In the Minnesota counties, Green and Janssen (1975) stated that during the summer this hawk is "most numerous in the north central, northeastern . . . regions."

Winter: Uncommon to rare winter resident in the Western Upland and Central Plain. Casual in midwinter in the Northern Highland. Three were observed on Solon Springs (Douglas County) CBC on 30 December 1973.

Habitat: The Polk County nest was situated about 4.6 m from the ground in an aspen tree. Surrounding vegetation consisted of young aspen–maple–basswood forest, intermixed with red pine. Additional summer observations have been made in similar habitat and in brushy "edge" situations. This hawk is usually observed in oak–maple woodlots along the St. Croix River during winter. Occasionally, an individual will frequent feeding stations in residential areas.

Cooper's Hawk (*Accipiter cooperii*)

Status: Regular migrant, nesting species, and winter resident. The WDNR has listed this species as threatened (Les 1979). Alteration of nesting habitat resulting from intensive farming is a primary cause for their decline.

Migration: Uncommon to rare migrant throughout the Valley. Spring migration begins in mid-March; birds are most frequently encountered 10–25 April. Nonsummering birds have departed by 15 May. Fall migration begins in late August and continues through mid-October. Because of the low number of birds observed during fall migration, no indication of peak movements is provided.

Nesting Season Distribution: Rare nesting species throughout the Valley. Although this hawk is regularly observed during the summer, only two confirmed nesting records exist. On 13 June 1976 a nest containing two young, and on 29 June 1976 a nest containing one young, were found 8 km west and 4.8 km east of Star Prairie, St. Croix County. Goddard (1972) reported one pair during the breeding season in Pierce County and Jackson (1941) reported a breeding season record (31 May 1919) for Burnett County. Numerous other breeding season records exist, but data on eggs or young are lacking.

Winter: Rare winter resident in the Western Upland; casual to absent elsewhere.

Habitat: Both St. Croix County nests were in second-growth red oak woodlots, bordered by brushy fencerows. I have observed this species during the breeding season in similar second-growth habitats and in mixed jack pine–oak situations in Burnett and Pine counties. Wintering birds are regularly observed occupying Lowland Deciduous Forest habitats during this period. Like the sharp-shinned hawk, this species will occasionally frequent bird feeding stations in residential areas during the winter.

Red-tailed Hawk (*Buteo jamaicensis*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common (locally abundant) migrant throughout the Valley. During both seasons, large numbers of migrants can be observed associated with the St. Croix River and at Crex Meadows Wildlife Area, Burnett County. Spring migration begins in mid-February in the Western Upland and Central Plain, reaching the Northern Highland about 1 March. Peak spring movements occur 20 March to 15 April, and nonbreeders have departed by 1 May. Fall migration begins in mid-August with dispersal of juveniles from nesting areas. Peak fall movements occur 20 September to 10 October in the Northern Highland and throughout October elsewhere. Nonwintering birds have departed by 1 December.

Nesting Season Distribution: Common nesting species in all regions, most conspicuous in agricultural areas. Nest records have been obtained for all counties except Chisago. Analysis of Breeding Bird Survey data indicate that the red-tailed hawk is the most frequently encountered breeding hawk in the Western Upland and Central Plain.

Winter: Fairly common to uncommon winter resident in the Western Upland. Uncommon to rare in the Central Plain and rare to absent in the Northern Highland. Birds normally depart the northern regions by mid-January. In open agricultural areas along the lower St. Croix River, red-tailed hawks are the most frequently encountered hawk during the winter.

Habitat: Red-tailed hawks use a large variety of habitats during the nesting season. In agricultural areas this hawk will use brushy field margins, small woodlots, and woods edge situations. In the Northern Highland, the species is usually associated with field borders of extensive Northern Deciduous Forest and Coniferous Forest. Jack Pine Barren and Lowland Deciduous Forest probably receive the lowest frequency of use by nesting red-tailed hawks.

Red-shouldered Hawk (*Buteo lineatus*)

Status: Regular migrant, nesting species, and winter resident. The Wisconsin DNR has listed this species as threatened (Les 1979). Habitat destruction is considered the primary reason for their decline.

Migration: Uncommon to rare migrant in the Western Upland and Central Plain; rare to absent in the Northern Highland. Spring migration begins in mid-February with a gradual movement into the Western Upland along the St. Croix River. Migrants have reached the Central Plain by 25 March (earliest—11 March 1950, 16 March 1975; Polk County). Red-shouldered hawk migration is rather diffuse, consisting primarily of movements of solitary individuals. Consequently, determination of peak dates is difficult. Most birds have reached nesting territories by mid-April. Fall migration is equally diffuse, consisting of a gradual movement from nesting areas. During fall, red-shouldered hawks are most conspicuous throughout October and nonwintering birds have departed by 1 December.

Nesting Season Distribution: Uncommon and local nesting species in the Western Upland and Central Plain, rare and local in the Northern Highland. A. C. Rosenwinkel found young in a nest along the Willow River, Pine County, on 7 April 1949 (Mierow 1949). Establishment of the red-shouldered hawk as a nesting bird in the Valley is apparently very recent. Roberts (1932) mentioned no nests from Minnesota, and cited only one summer record (3 July 1927, at Marine-on-St. Croix, Washington County). Behavior and plumage of that bird suggested nesting. Since that time, however, the red-shouldered hawk has been recorded regularly, and there are presently nest records for all the counties except Douglas.

Winter: Rare and local winter resident of Lowland Deciduous Forests in the Western Upland, casual elsewhere.

Habitat: Primarily a species of medium-aged to mature Lowland Deciduous Forest. Rarely encountered away from this habitat type during the breeding season. S. D. Robbins and I recorded one red-shouldered hawk, apparently on territory, in mature black spruce habitat near Range, Polk County, on 16 March 1975.

Broad-winged Hawk (*Buteo platypterus*)

Status: Regular migrant and nesting species.

Migration: Fairly common spring and common fall migrant throughout the Valley. During peak fall migration, broad-winged hawks are occasionally abundant at the Crex Meadows Wildlife Area, Burnett County. Spring migrants arrive in the Western Upland and Central Plain in early April (earliest—26 March 1975, St. Croix County; 24 March 1968, Chisago County). Migrants arrive in the Northern Highland 5–10 April (earliest—21 March 1956, Burnett County). Peak spring migration occurs 15 April to 1 May, and nonbreeders depart by 20 May.

Fall migration begins in late August, with dispersal from nesting areas and formation of loose flocks. Peak fall migration occurs 10–25 September, when 400 to 500 individuals can be observed on good flight days. Movement is very rapid, and departure from the region occurs by 10 October.

Nesting Season Distribution: Common nesting species throughout the Northern Highland and northern tier of the Central Plain. Fairly common in the remainder of the Central Plain. Rare and local in the Western Upland. Nest records exist for all counties of the Valley except Pierce. In the Northern Highland, the broad-winged hawk must be considered the most abundant and conspicuous nesting raptor. Roberts (1932), quoting Surber (1919), stated that along the St. Croix River in Pine County, the broad-winged hawk was "the commonest hawk" in the region.

Habitat: Broad-winged hawks use a variety of coniferous and deciduous forest types for nesting. Regularly used habitats in the Northern Highland and Central Plain include Northern Upland Deciduous Forest, Upland Coniferous Forest, and mixed deciduous–coniferous forest. Jack Pine Barren and jack pine–oak habitats are also occupied, but to a lesser extent. Nesting broad-winged hawks have been found occupying Southern Deciduous Forest and Lowland Deciduous Forest in the Western Upland.

Swainson's Hawk (*Buteo swainsoni*)

Status: Casual migrant throughout the region, regular in St. Croix County. Several recent summer records.

Migration: Rare and local migrant with records from all regions. Spring migration dates range from 3 April 1965 (Burnett County) to 20 May 1967 (Pine County). Most records occur between 20 April and 15 May. Fall migration records are fewer and range from 6 August 1975 (Burnett County) to 12 October 1968 (Polk County). Most fall migration records occur 25 August to 10 September.

Nesting Season Distribution: During June and July 1978, up to three separate pairs were observed regularly in St. Croix and northern Pierce counties. Specifically, these pairs were near Oakridge Lake and near Erin Corners in St. Croix County, and near the junction of County Highway W and Highway 29, 10 km west of River Falls in Pierce County. Attempts to locate nests failed. These summer records are especially noteworthy because nesting occurs yearly in nearby areas of Dakota County, Minnesota (Green and Janssen 1975).

Habitat: Most Swainson's hawks observed during migration are associated with open habitats including Managed Grasslands and agricultural fields. The birds observed in June and July 1978 were in an ecotone between Managed Grassland and Southern Deciduous Forest. The Pierce County pair was using a hayfield–woods ecotone.

Rough-legged Hawk (*Buteo lagopus*)

Status: Regular migrant and winter resident, accidental in summer.

Migration: Fairly common migrant throughout the Valley, becoming common at Crex Meadows, Burnett County, during the fall and early winter. Fall migrants arrive about 20 September (earliest—4 September 1974, Burnett County; 15 September 1968, Pine County). Peak fall migration occurs 20 October to 15 November, with a gradual exodus from most northerly locations occurring until 1 January. Spring migration begins in late February in the Western Upland and migrants have reached the Northern Highland by 20 March. Peak spring migration occurs 15 March to 15 April and departure by 15 May (latest—7 June 1975, Burnett County; 12 June 1975, St. Croix County).

Winter: Regular winter resident in the Western Upland and Central Plain. Sporadic midwinter resident in the Northern Highland. Distribution and abundance of wintering birds is highly dependent on small mammal populations and the severity of the weather.

Habitat: Rough-legged hawks occupy open habitats almost exclusively. Edges of agricultural fields, hayfields, native grasslands, and wet meadows receive primary use. Occasionally, this hawk will be found in Northern Hardwood and Lowland Deciduous Forests.

Ferruginous Hawk (*Buteo regalis*)

Status: Casual fall visitor.

Records: W. Norling observed an adult at the Fish Lake Wildlife Area, Burnett County, on 25 October 1974. I observed an adult flying over the Oakridge Waterfowl Production Area, St. Croix County, on 24 September 1978. A 30 December 1967 record of a ferruginous hawk on the Suburban St. Paul

CBC is questioned, primarily because of the date and because the only accompanying notes were "all field marks were noted."

Golden Eagle (*Aquila chrysaetos*)

Status: Regular migrant and winter resident.

Migration: Rare migrant throughout the Valley becoming uncommon at Crex Meadows, Burnett County, in the fall. Fall migration begins about 5 October; most records are from 10 October to 15 December (earliest records—3 August 1976, 4 September 1974, and 15 September 1972; Crex Meadows, Burnett County). Peak migration occurs 1 November to 1 December. Spring migration begins in mid-February with a gradual movement through the Valley. Peak migration occurs 1–15 March and departure by 1 April (latest—2 May 1975; Crex Meadows, Burnett County).

Winter: Very rare and local winter resident throughout the Valley. Usually the largest numbers are observed at Crex Meadows, Burnett County, where up to four individuals occur throughout the winter.

Habitat: At Crex Meadows, golden eagles are usually associated with the large areas of restored native prairie on the refuge portion of the wildlife area. Elsewhere in the Valley, wintering birds primarily use open agricultural fields.

Bald Eagle (*Haliaeetus leucocephalus*)

Status: Regular migrant, nesting species, and winter resident. This species is listed as threatened by the U.S. Fish and Wildlife Service. The WDNR has listed this species as endangered (Les 1979). Pesticides, nest-site destruction, and indiscriminate shooting are the main reasons for their decline.

Migration: Uncommon migrant throughout the Valley, fairly common at Crex Meadows, Burnett County. Spring migration begins in mid-February with a gradual movement from wintering areas along the lower St. Croix River. Peak spring migration occurs 10–25 March; most adults are on breeding territories by 1 April. Spring migration extends into early May; subadults arrive considerably later than adults.

Fall migration begins in late August, when juveniles move away from nesting areas. Peak fall migration occurs in two stages. Subadults reach peak numbers 1 October to 1 November and adults peak 15 October to 1 December. Most birds have departed by 15 December. Largest concentrations of migrants occur at Crex Meadows, Burnett County, and in areas directly adjacent to the St. Croix River.

Nesting Season Distribution: Rare nesting species throughout the Valley; nesting has been reported in Chisago, Burnett, Douglas, Pine, Pierce, and Polk counties. The Pierce County nesting pair was associated with the lower Kinnickinnic River. The pair abandoned their territory after a June 1973 storm destroyed the nest tree. Breeding populations in the St. Croix River Valley have been monitored continuously since the mid-1960's, and there is recent evidence that the population may be increasing.

Winter: Fairly common winter resident primarily in the vicinity of open water. Wintering birds at Crex Meadows regularly occupy open prairie areas. The distribution of wintering bald eagles closely follows the large river systems of the Valley; birds are located primarily at Prescott (Pierce and Washington counties) and St. Croix Falls (Polk and Chisago counties) along the St. Croix River, the Kettle River (Pine County), and Gordon Flowage (Douglas County).

Habitat: Nesting habitat of bald eagles consists of a complex of deciduous, coniferous, wetland, and shrub situations. In all instances, however, two prominent features (tall pine trees and nearby lakes or large rivers) occur. Unfortunately for the eagles, these are two conditions that also attract man, and several nesting territories in the Valley are endangered because of human encroachment.

Marsh Hawk (*Circus cyaneus*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Fairly common migrant throughout the Valley, common at Crex Meadows, Burnett County. Spring migrants arrive in the Western Upland about 15 March; average arrival is about 20 March. Migrants arrive in the Northern Highland about 25 March. Peak migration occurs 1–20 April, and nonbreeders depart by 1 May. Fall migration begins in mid-August and consists primarily of juveniles. Peak fall migration occurs 15 September to 15 October in the Central Plain and extends to 25 October at Crex Meadows. Most birds have departed by 15 November.

Nesting Season Distribution: Uncommon nesting species throughout the Valley, with nesting records for all counties. Apparently less numerous at present than earlier as evidenced by Jackson (1941), who reported them as "generally distributed . . . in favorable environments throughout the region." Marsh hawks have been greatly reduced as a nesting bird in western Wisconsin since the mid-1960's.

Winter: Casual midwinter resident in the Western Upland. Two midwinter records for Crex Meadows, Burnett County (9 February 1954, 25 February 1953).

Habitat: Marsh hawks use a wide range of grassland habitat types for nesting. Nesting birds have been recorded in retired cropland (timothy–quackgrass), old field habitat, wetlands (primarily sedge meadows), and restored prairie. In areas of intensive agriculture, nesting may regularly occur in hayfields and occasionally in oat fields.

FAMILY PANDIONIDAE: Ospreys

Osprey (*Pandion haliaetus*)

Status: Regular migrant and nesting species. The WDNR listed the species as endangered (Les 1979). Residual pesticides and loss of nesting habitat are considered reasons for their decline.

Migration: Uncommon migrant throughout the Valley, most regularly observed adjacent to the St. Croix River. Spring migrants arrive during the second week of April (earliest—22 March 1953, Burnett County and 26 March 1967, Washington County). Peak abundance of spring migrants occurs between 25 April and 5 May. Fall migration begins with departure from nesting areas in mid-August. Peak fall migration occurs 25 August to 15 September and departure by 10 October (latest—23 November 1968, Chisago County).

Nesting Season Distribution: Ospreys are rare and local nesting species north of St. Croix and Washington counties. The largest concentration of breeding adults is near the Crex Meadows Wildlife Area in Burnett County. Sindelar (1971) observed at least four nests in Burnett and three in Polk counties in the late 1960's.

Winter: M. R. Olson observed an osprey near Hudson, St. Croix County, on 31 December 1970.

Habitat: Nesting ospreys use a variety of habitat types including acid bogs, open lakes, and riverbanks. One of the most important habitat requirements is the presence of dead trees used for nest sites. Variations occur in the size of the water body that attracts breeding pairs. Most breeding pairs I have observed nest near a small lake (usually <20 ha), within 1.6 km of larger lakes. Large bodies of water within proximity of a nesting site serve as important feeding areas for nesting ospreys.

FAMILY FALCONIDAE: Falcons

Gyrfalcon (*Falco rusticolus*)

Status: Accidental, one record.

Record: One was observed near Marine-on-St. Croix, Washington County, on 24 December 1973 (Honetschlager 1974).

Peregrine Falcon (*Falco peregrinus*)

Status: Regular migrant and former nesting species. The U.S. Fish and Wildlife Service and WDNR (Les 1979) have listed this species as endangered. Pesticides, habitat loss, and human harassment are among the major causes of the decline.

Migration: Rare migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 April (earliest—4 April 1974, Pierce County) and the Northern Highland 15–20 April. Departure from the Valley occurs 15–20 May. Fall migrants arrive 5–10 September and most observations occur during 15–30 September and departure by 15 October. During fall migration, the restored prairie on the refuge portion of Crex Meadows is the most consistent area in the Valley to observe this raptor.

Nesting Season Distribution: Formerly a rare and local nesting bird along the St. Croix River. Roberts (1932) reported that fewer than six pairs nested along the upper St. Croix River in the late 1920's. Surber (1919) reported a pair of peregrine falcons along the St. Croix River near the mouth of the Tamarack River (Pine County) during July 1918. Jackson (1941) did not report this species during the 1919 nesting season in northwestern Wisconsin. Apparently the last known nesting attempt occurred along "the upper St. Croix River" in 1945 (Green and Janssen 1975).

Habitat: Roberts' (1932) description of peregrine falcons nesting "along the bluffs" of the St. Croix River is all that is known of their nesting habitat in the Valley. Peregrine falcons presumably nested on the relatively inaccessible rock ledges on the sides of the steepest bluffs. During migration, most peregrine falcons are observed in association with mudflats on large natural and man-made wetlands. Open mudflats support migrant shorebirds and waterfowl and provide excellent hunting for falcons.

Merlin (*Falco columbarius*)

Status: Regular migrant and casual summer resident.

Migration: Rare migrant throughout the Valley. Spring migrants arrive in the Western Upland about 5–10 April and the Northern Highland 10–15 April. During spring migration the merlin is most frequently observed 1–15 May and departs by 25 May (latest—28 May 1977, St. Croix County). Fall migrants arrive 25 August to 5 September and are most frequently observed 10–25 September. Departure from the Northern Highland occurs 1–10 October and elsewhere by 20 October.

Nesting Season Distribution: Casual summer resident, restricted to the Northern Highland. Jackson (1941) mentioned the observation of an adult at Gordon (Douglas County) on 28 July 1919. I observed an adult merlin near Moose Junction (Douglas County, Sec. 14, T. 44 N., R. 15 W.) on 30 June 1975 and 8 July 1977. Both observations were of lone birds. These dates provide speculation of possible nesting, although neither nests nor young have been observed.

Habitat: My Douglas County observations were made in a large stand of Lowland Coniferous Forest. Predominant vegetation included trembling aspen, green ash, black spruce, and balsam fir. These vegetative characteristics are usually associated with merlin breeding habitat in their normal breeding range in the boreal forest region of southern Canada. During migration, merlins regularly use a variety of both open and forested habitats.

American Kestrel (*Falco sparverius*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant in the Western Upland and Central Plain, common in the heavily forested regions of the Northern Highland. Spring migrants arrive in the Western Upland about 5–15 March and the Northern Highland 25 March to 5 April. Peak abundance through the Valley occurs 10–25 April. Fall migration begins in mid-August and peak abundance occurs 1–15 September. Most fall migrants have departed the Northern Highland by 15 October and elsewhere by 15 November.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, uncommon and more local in the Northern Highland.

Winter: Casual midwinter resident in the Central Plain and Western Upland.

Habitat: Primarily associated with scattered tree groves in agricultural areas, brushy edges of deciduous forest, and Old Field Community in southern areas. In the Northern Highland, American kestrels use edge situations associated with agricultural clearings, and areas that are managed for wildlife production. Wintering American kestrels are usually found along roadsides hunting from transmission wires and occasionally near feeding stations in residential areas.

FAMILY TETRAONIDAE: Grouse

Spruce Grouse (*Canachites canadensis*)

Status: Formerly a permanent resident, two recent records.

Distribution: Scott (1943*b*) reported that spruce grouse were last reported in 1928 or 1929 from the town of Dairyland (T. 43 N., R. 14 W.), Douglas County. Scott believed that at one time this species probably occurred throughout northern Wisconsin and south along the St. Croix River. The presumed range in Wisconsin extended south to central Polk County. Despite the presence of suitable spruce habitats in Pine County, this species is not known south of central St. Louis County in Minnesota (Green and Janssen 1975).

On 26 May 1978, R. Hoffman (personal communication) observed one spruce grouse in Sec. 33, T. 42 N., R. 15 W., Burnett County. Returning to the same area on 4 September 1978, Hoffman again observed a single spruce grouse.

Habitat: Scott (1943*b*) reported that spruce grouse are "almost always found only in spruce-balsam swamps" (= Lowland Coniferous Forest).

Ruffed Grouse (*Bonasa umbellus*)

Status: Regular permanent resident.

Distribution: Common resident in the Northern Highland and in the northern half of the Central Plain. Fairly common in the oak forests of the Central Plain and Western Upland. Breeding populations experience yearly fluctuations that are almost predictable. Attempts to correlate these fluctuations with changes in food availability have proved unsuccessful thus far.

Habitat: Nesting ruffed grouse occur in a variety of upland deciduous forest types. In the Northern Highland and parts of the Central Plain, ruffed grouse are most commonly associated with medium-aged aspen forests that contain scattered openings. In the Western Upland and areas of the Central Plain adjacent to the St. Croix River, nesting ruffed grouse are associated with medium-aged oak forests and woodlots. A well-developed shrub layer consisting of prickly ash, thorn apple, and beaked hazel is usually associated with high-quality ruffed grouse habitat.

Greater Prairie Chicken (*Tympanuchus cupido*)

Status: Extirpated as a natural breeding species; reintroduced in 1974.

Former Distribution: Until the late 1890's, the greater prairie chicken was an abundant species on the prairies of Pierce and St. Croix counties and ranged north to Grantsburg, Burnett County. Schorger (1943) summarized numerous accounts of the status of this species including newspaper accounts of abundance. Populations appeared to remain at high levels through 1865. The winter of 1873 was reportedly very severe and St. Croix County farmers reported the winter was extremely hard on the greater prairie chicken. Populations fluctuated considerably after 1875.

Reduced numbers of greater prairie chickens remained in St. Croix County until the 1920's, although they were still well distributed between Hammond and New Richmond. The last greater prairie chicken observed in St. Croix County was shot near Hammond in 1932. At Crex Meadows, the last greater prairie chicken reported on a booming ground was observed in April 1949.

Former status of the greater prairie chicken in the Minnesota counties is poorly known. Roberts (1932) made no reference to this species in three counties considered in the present report. Greater prairie chickens were known to breed in the vicinity of the Twin Cities at the time of Roberts. A limited amount of information is provided by Partch (1970) in summarizing the demise of this species in central Minnesota. Partch shows that greater prairie chickens were common or abundant in southern Washington County in 1849. Dispersal north through the Valley probably happened in the "late 1800's." This movement northward along the St. Croix was attributed to logging and fires creating favorable openings in sandy areas. Surber (1919), in describing an area of Pine County, stated that greater prairie chickens near Hinckley occurred "in goodly numbers" in 1919. He made an appeal to local residents to report illegal shooting so the "overflow" (of chickens) into surrounding areas would manifest another hunting season.

Current Distribution: The WDNR began a greater prairie chicken reintroduction program at Crex Meadows during October 1974. This project met with limited success during the first 2 years. In 1977, at least one female was observed with a brood near the original release site. Continued research and habitat management at Crex Meadows may prove essential in the restoration of this species in portions of its former breeding range.

Sharp-tailed Grouse (*Pedioecetes phasianellus*)

Status: Regular permanent resident.

Distribution: Sharp-tailed grouse were formerly well distributed throughout the Valley, with nest records from Pine, Polk, and St. Croix counties. Currently sharp-tailed grouse occur in northern Polk, central Burnett, eastern and central Pine, and southwestern Douglas counties. The largest breeding populations occur at Crex Meadows, Burnett County, and on the sharp-tailed grouse management area near Solon Springs, Douglas County. Dancing ground surveys from Crex Meadows indicate a fairly stable population, with at least eight active dancing grounds in 1976 (WDNR files).

Away from the center of the sharp-tailed grouse breeding range, this species is still occasionally observed in St. Croix County. A flock of 12 was observed near Roberts on 13 October 1976, and a single bird observed near Star Prairie on 1 November 1977.

Habitat: Sharp-tailed grouse are characteristic of mixed grasslands containing small groves of oak or aspen trees or shrubs. At the grouse management area in Douglas County, small patches of jack pine are commonly interspersed with grasslands. Most well-known sharp-tailed grouse breeding habitat in the Valley is characterized by restored prairie grasses on loose sandy soils.

FAMILY PHASIANIDAE: Quails and Pheasants

Bobwhite (*Colinus virginianus*)

Status: Regular permanent resident.

Distribution: The Valley is at the extreme northern limit of the bobwhite range. A very rare resident, restricted to Washington, St. Croix, and Pierce counties. Recent summer records from Crex Meadows in Burnett County are probably released birds. Additionally, Green and Janssen (1975) report records of bobwhites in Pine County. Habitat loss coupled with winter stress have created a severe impact on bobwhite populations.

Habitat: Primary bobwhite habitat includes retired agricultural fields and Old Field Community intermixed with hedgerows and scattered shrubs. Much of this habitat continues to be altered or destroyed by expanding agricultural and urban development.

Ring-necked Pheasant (*Phasianus colchicus*)

Status: Introduced permanent resident.

Distribution: Fairly common resident of the Western Upland and Central Plain, rare to absent in the Northern Highland. Ring-necked pheasants were first introduced in western Wisconsin during the 1930's. Populations remained fairly stable through the 1950's and 1960's, primarily because of yearly releases by State wildlife agencies. Currently, ring-necked pheasant populations are reduced because of farming practices that eliminated most of their habitat. Urban expansion has not impacted this species to nearly the extent that agricultural production has. Green and Janssen (1975) stated that the largest populations remaining in Minnesota exist in the Twin Cities metropolitan area.

Habitat: The ring-necked pheasant is a species of agricultural areas, primarily edge habitats including field margins, fencerows, retired cropland, Old Field Communities, and heavily vegetated wetlands. Ring-necked pheasants in the Central Plain have shown an encouraging response to Managed Grasslands that are maintained for duck production.

Gray Partridge (*Perdix perdix*)

Status: Introduced permanent resident.

Distribution: Rare resident of the Western Upland. The small population that exists in the Valley is largely restricted to a small area of central St. Croix County. The largest population occurs near the village of Roberts in T. 29 N., R. 18 W.; T. 29 N., R. 17 W.; and T. 30 N., R. 17 W. Distribution of the population in the Minnesota counties is poorly known, although Mettler (1977) showed that the species range included southern Washington County. McCabe and Hawkins (1946) reported a population density of 0.6 coveys per 62 km in St. Croix County.

Habitat: The gray partridge is primarily a species of croplands and adjoining edge habitat. Preferred habitats include corn and oats fields, weedy edges of summer fallow, and remnant patches of native prairie along railroad rights-of-way that border agricultural fields.

FAMILY GRUIDAE: Cranes

Sandhill Crane (*Grus canadensis*)

Status: Regular migrant and nesting species.

Migration: Rare migrant throughout the Valley, locally common at Crex Meadows, Burnett County. Sandhill cranes have been observed in Washington County on four occasions: 31 March 1967, 9 April 1970 and 1971, and 20 November 1970. Three records exist for St. Croix County: 17 April 1947, 4 May 1974, and 30 October 1977. There is one record (29 April 1950) for Polk County.

The most reliable data on migration is from Crex Meadows, where the average date of spring arrival is 4 April (earliest—25 March 1976). Peak spring concentration occurs about 20 April. During fall migration, the first migrants arrive in early September and peak abundance is 15 October to 1 November. During this period, concentrations of 150 to 200 individuals commonly occur on the refuge portion of Crex Meadows; high counts were 350 on 19 October 1975 and 420 on 30 October 1977. Departure of fall migrants occurs soon after freeze-up; the latest was on 18 November 1962.

Nesting Season Distribution: The first reported nesting in the Valley occurred in the Kohler–Peet area north of Crex Meadows along the St. Croix River in 1903. Roberts (1932) mentioned a local farmer reported sandhill cranes nesting in Burnett County from 1904 through 1930. Recent summer observations indicate that cranes still probably nest at Kohler–Peet; however, nests or young have not been observed.

Currently, sandhill cranes are fairly common during the nesting season at Crex Meadows. Recent surveys indicate that 30 to 40 pairs are nesting at that location. Elsewhere, Green and Janssen (1975) cited a 1950 nest record near Beroun, Pine County. Johnson (1976) reported breeding season sandhill cranes in Thunder Meadow and the St. Croix River marshes, Pine County, and in the extensive marshes of the Carlos Avery Wildlife Management Area, Chisago County, during 1974–75. Henderson (1978) showed that breeding season sandhill cranes occurred in three Pine County townships: T. 42 N., R. 16 W.; T. 41 N., R. 13 W.; and T. 38 N., R. 17 W.

Habitat: Breeding sandhill cranes are typically associated with large expanses of Northern Sedge Meadow characterized by tussock sedge, bristly sedge, fox sedge, bluejoint grass, rattlesnake grass, marsh cinquefoil, and marsh bellflower.

FAMILY RALLIDAE: Rails, Gallinules, and Coots

King Rail (*Rallus elegans*)

Status: Casual spring migrant and nesting species.

Migration: Rare spring migrant near the St. Croix River. Spring arrival dates range from 24 April 1977 in St. Croix County to 9 May 1958 in Burnett County. Fall migration records are not available.

Nesting Season Distribution: Observations at Crex Meadows, Burnett County, include 12 June 1969, 25 June 1975, 27 and 28 June 1956, 3 July 1963, and 12 August 1970. These breeding season records suggest possible nesting although nests or young have not been found. In St. Croix County, I observed a male king rail at East Twin Lake on 17 June 1976. Green and Janssen's (1975) Washington County record is the only confirmed nesting observation in the Valley.

Habitat: King rails at Crex Meadows are usually associated with dense cattail vegetation in man-made impoundments.

Virginia Rail (*Rallus limicola*)

Status: Regular migrant and nesting species, one winter record.

Migration: Common migrant in St. Croix, Polk, and Washington counties, uncommon to rare elsewhere. Spring migrants arrive about 25 April (earliest—16 April 1958, Burnett County): peak abundance is 10–15 May. Peak fall migration occurs between 20 September and 1 October and departure by 30 October.

Nesting Season Distribution: Fairly common nesting species in prairie wetlands of St. Croix, Polk, and Washington counties. Uncommon to rare nesting species elsewhere in the Valley. One nest record was reported for Pine County in 1969 (Russell 1969).

Winter: One individual was observed on 30 December 1978 in Washington County (Suburban St. Paul CBC).

Habitat: Virginia rails use a variety of wetland classes for nesting. Greatest densities occur in seasonally and semipermanently flooded wetlands with cattail, river bulrush, and phragmites the predominant vegetation. Nesting Virginia rails are occasionally found in Northern Sedge Meadow habitats, along well-vegetated streams and in Shrub Carr wetlands.

Sora (*Porzana carolina*)

Status: Regular migrant and nesting species.

Migration: Common migrant in prairie wetlands of St. Croix, Polk, and Washington counties and at Crex Meadows in Burnett County. Fairly common to uncommon elsewhere. Spring migrants arrive about 25 April (earliest—6 April 1964, Burnett County), reaching peak abundance 15–20 May. Peak abundance during fall migration occurs 10 September to 10 October and departure by 5 November.

Nesting Season Distribution: Common nesting species in prairie wetlands in the Western Upland and Central Plain, and at Crex Meadows. Uncommon elsewhere.

Habitat: Soras use a variety of wetland types for nesting. Highest densities occur in seasonally and semipermanently flooded wetlands where cattail, river bulrush, and softstem bulrush are the predominant vegetation types. Soras also use wetlands that are more acidic, containing various species of waterlilies and pickerelweed. During high water periods, nesting soras also use sedge meadows.

Yellow Rail (*Coturnicops noveboracensis*)

Status: Casual migrant and summer resident.

Migration: S. D. Robbins observed this species twice in central St. Croix County: 26 April 1961 and 17 May 1963. At Crex Meadows, Burnett County, apparent migrants were observed on 25 May 1976, 30 May 1977, and 28 May 1978. R. Hoffman observed one at the Fish Lake Wildlife Area, Burnett County, on 26 May 1979.

Nesting Season Distribution: The first record of the yellow rail in the Valley was obtained on 23 June 1962, when N. R. Stone observed a single bird at Crex Meadows (Robbins 1963). During the summers of 1976 and 1977, yellow rails were again heard calling in a large Northern Sedge Meadow at Crex Meadows. Although these birds were observed during normal nesting periods, neither nests nor young were observed. Continued observations at

Crex Meadows may shed additional light on the breeding status of this species.

Common Gallinule (*Gallinula chloropus*)

Status: Casual migrant and nesting species.

Spring Records: Gallinules were observed at Crex Meadows, Burnett County, on 9 May 1958 and 10 May 1976. In St. Croix County spring records include 16 May 1961 and 25 May 1976. Washington County records range from 15–30 May.

Nesting Season Distribution: Green and Janssen (1975) showed a nesting record for Washington County. Since 1975, I have found common gallinule during the nesting season near Lake Elmo, Washington County. In Wisconsin, one bird was observed at Crex Meadows on 11 June 1958. The first St. Croix County nesting record was obtained on 9 July 1976 near Star Prairie. On 14 July 1977 an adult with a brood of three was observed on a wetland near Hudson. Additionally, a single adult was observed near Roberts on 11 August 1975.

Habitat: Most common gallinules observed during the nesting season are associated with seasonally and semipermanently flooded wetlands. These wetlands typically support an abundant submerged and emergent flora.

American Coot (*Fulica americana*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Abundant migrant throughout the Valley. Spring migrants arrive in the Western Upland about 10 March reaching the Northern Highland 1–10 April. Peak spring abundance occurs between 20 April and 1 May. The first fall migrants arrive between 1 and 10 September. Peak fall abundance occurs 25 September to 10 October and departure by 15 November.

Nesting Season Distribution: Common nesting species on prairie wetlands in St. Croix, Polk, and Washington counties. Fairly common nesting species at Crex Meadows in Burnett County. Uncommon to rare elsewhere during the nesting season.

Winter: Casual early winter resident along the St. Croix River. Afton CBC records include one each on 1 January 1957, 1971, 1972, 1974, and 1975. I observed one along the Apple River, St. Croix County, on 19 December 1977. During the winter of 1975–76, a single bird remained on the St. Croix River near Bayport, Washington County.

Habitat: American coots are characteristic of seasonally and semipermanently flooded wetlands. Predominant vegetation associated with American coot nesting habitat includes cattail, river bulrush, softstem and hardstem bulrush, burreed, and phragmites. Nesting also occurs to a more limited extent on lower quality acidic wetlands characterized by waterlily and pickerelweed. Very few nesting pairs are found on riverine habitats.

FAMILY RECURVIROSTRIDAE: Stilts and Avocets

American Avocet (*Recurvirostra americana*)

Status: Casual migrant.

Records: There are three records from Crex Meadows, Burnett County: 30 April 1971, 16 May 1977, and 22 August 1965. One American avocet was observed in St. Croix County near New Richmond on 13 May 1973.

FAMILY CHARADRIIDAE: Plovers

Semipalmated Plover (*Charadrius semipalmatus*)

Status: Regular migrant.

Migration: Fairly common migrant in the Western Upland and Central Plain, rare to absent in the Northern Highland. The first spring migrants arrive 25 April to 1 May (earliest—19 April 1976, St. Croix County). Peak abundance occurs 10–20 May and departure by 25 May. The first fall migrants arrive between 25 July and 1 August. Peak fall populations occur 20 August to 1 September and departure by 25 September.

Habitat: Most common on seasonally flooded wetlands. Uncommon on lakeshores and in short vegetation associated with semipermanently flooded wetlands.

Piping Plover (*Charadrius melodus*)

Status: Accidental, two records.

Records: S. D. Robbins observed a single piping plover near Roberts, St. Croix County, from 3 to 15 May 1967 (Robbins 1968). S. V. Goddard found one on the same wetland on 12 May 1972 (Faanes and Goddard 1976).

Killdeer (*Charadrius vociferus*)

Status: Regular migrant and nesting species, casual in early winter.

Migration: Abundant migrant in the Western Upland and Central Plain, common and more local in the Northern Highland. Spring migrants arrive about 15 March (earliest—2 March 1961, Burnett County); peak abundance is 10–25 April. Fall migration begins about 10 August. Peak abundance occurs 1–15 September and departure by 1 November.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, uncommon to rare and local in the Northern Highland.

Winter: There are eight early winter records for an area in Washington County; the dates are from 15 to 30 December. S. D. Robbins observed one in St. Croix County on 16 January 1964.

Habitat: Killdeer use a variety of habitats ranging from cropland, summer fallow, pastures, shorelines, and lawns to flat-topped roofs in residential areas.

American Golden Plover (*Pluvialis dominica*)

Status: Regular migrant.

Migration: Fairly common spring and rare fall migrant in the Western Upland, locally common during spring migration at Crex Meadows, Burnett County. Rare to absent elsewhere. Spring migrants arrive 20–25 April. Peak abundance occurs 10–15 May and departure by 1 June. Fall migrants arrive about 20 August and have departed by 15 October (latest—2 November 1965, St. Croix County).

Habitat: Most commonly observed in temporarily flooded cornfields, alfalfa, or oat stubble, and are less common on mudflats and lakeshores. This plover uses habitat that is fairly dry and usually away from the edge of wetland basins.

Black-bellied Plover (*Pluvialis squatarola*)

Status: Regular migrant.

Migration: Uncommon migrant in the Western Upland and Central Plain. Locally common during spring at Crex Meadows, Burnett County, rare to absent in the Northern Highland. Spring migrants arrive about 5 May (earliest—15 April 1975, St. Croix County). Peak abundance occurs 15–20 May and departure by 1 June. Fall migrants arrive 10–20 August. Peak abundance occurs 5–20 September and departure by 15 October (latest—3 November 1976, St. Croix County).

Habitat: Unlike the preceding species, the black-bellied plover commonly uses temporarily flooded wetlands. Less common on flooded alfalfa or oat stubble and along the edge of semipermanently flooded wetlands.

FAMILY SCOLOPACIDAE: Sandpipers and Phalaropes

Hudsonian Godwit (*Limosa haemastica*)

Status: Regular migrant.

Migration: Rare spring migrant in the Western Upland and at Crex Meadows, Burnett County. Most records are from central St. Croix and eastern Washington counties. There are no fall records. The first migrants arrive 5–10 May. Flocks as large as 40 individuals have been observed 15–20 May and departure occurs by 30 May.

Habitat: Most individuals are observed on temporarily flooded agricultural fields. Occasional use is made of flooded alfalfa fields and edges of man-made impoundments.

Marbled Godwit (*Limosa fedoa*)

Status: Regular migrant.

Migration: Rare and local migrant in the Western Upland and at Crex Meadows, Burnett County; most records are from central St. Croix County. Spring migrants arrive about 20 April. Peak numbers (five to seven) occur 1–10 May; departure is by 25 May. Fall migrants arrive about 25 July and depart by 1 September. W. Norling observed an injured marbled godwit at Grettum Flowage, Burnett County, on 8 November 1975.

Habitat: Observed primarily on temporarily flooded agricultural fields and along the edge of seasonally flooded wetlands.

Whimbrel (*Numenius phaeopus*)

Status: Accidental, one record.

Record: I observed one whimbrel along the north shore of East Twin Lake near Roberts, St. Croix County, on 17 May 1976.

Long-billed Curlew (*Numenius americanus*)

Status: Accidental, one record.

Record: N. R. Stone observed one long-billed curlew at Crex Meadows, Burnett County, on 25 May 1966 (Stone 1967).

Upland Sandpiper (*Bartramia longicauda*)

Status: Regular migrant and nesting species.

Migration: Rare spring and fall migrant in the Western Upland and Central Plain, casual to absent elsewhere. Spring migrants arrive 20–25 April. Because most observations are of solitary or paired birds, dates of peak abundance are difficult to establish. Fall migrants begin to arrive in late July and have departed by 15 September.

Nesting Season Distribution: Rare and local nesting species in suitable grass habitat in the Western Upland and Central Plain, locally common at Crex Meadows, Burnett County, and at the Sharp-tailed Grouse Management Area near Solon Springs, Douglas County. The latter site has been used since at least 1919, when Jackson (1942) found "a dozen or more." Green and Janssen (1975) considered the upland sandpiper "very scarce" in Pine County. One nest was found in Washington County in 1971. In northern Pierce and central St. Croix counties, this species was fairly common until 1972. Increased conversion of remaining grasslands, primarily related to ending the Soil Bank Program, has caused their apparent extirpation in these two counties.

Habitat: Characteristic nesting species of tallgrass prairie such as at the Sharp-tailed Grouse Area, Douglas County, and in sedge meadows. Also regularly observed in unmowed alfalfa and timothy fields.

Greater Yellowlegs (*Tringa melanoleucus*)

Status: Regular migrant.

Migration: Fairly common migrant in the Western Upland and Central Plain, uncommon in the Northern Highland. Spring migrants arrive 30 March to 10 April. Peak abundance occurs 20 April to 5 May and departure by 25 May. The first fall migrants arrive about 10 July (earliest—3 July 1963, Burnett County). Peak abundance occurs 10-20 August, and departure by 30 October (latest—7 November 1975 and 10 November 1963, Burnett County).

Habitat: Greater yellowlegs occur in a variety of wetlands, flooded grasslands, plowed agricultural fields, Northern Sedge Meadow, and along the edge of seasonally, semipermanently, and permanently flooded wetlands. Primary use is made of flooded agricultural fields.

Lesser Yellowlegs (*Tringa flavipes*)

Status: Regular migrant.

Migration: Common to locally abundant migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive in the Western Upland 30 March to 5 April and the Northern Highland 10-15 April. Peak abundance occurs 1-10 May and departure by 30 May. The first fall migrants arrive about 10 July (earliest—4 July 1975, St. Croix County and 5 July 1960, Burnett County). Peak abundance occurs 1-10 August and departure by 15 October (latest—8 November 1975 and 10 November 1963, Burnett County).

Habitat: Lesser yellowlegs occur in a variety of wetland types, flooded alfalfa fields, and agricultural fields. Primary use is made of flooded agricultural fields.

Solitary Sandpiper (*Tringa solitaria*)

Status: Regular migrant.

Migration: Uncommon migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Spring migrants arrive 25-30 April. Peak abundance occurs from 5-15 May and departure by 25 May. Fall migrants arrive 5-15 July. Peak fall abundance occurs 25 July to 20 August and departure by 25 September (latest—10 October 1969, Washington County).

Habitat: Primarily found on flooded agricultural fields and the muddy edges of wetlands. This species is occasionally observed in Northern Sedge Meadow and Shrub Carr wetlands.

Willet (*Catoptrophorus semipalmatus*)

Status: Regular migrant.

Migration: Rare migrant in the Western Upland, casual elsewhere. Spring migrants arrive about 30 April. Willets are most frequently observed 5–10 May and remain through 25 May. The first fall migrants arrive about 25 July and have departed by 1 September.

Habitat: Willets are found primarily on temporarily and seasonally flooded wetlands. K. H. Dueholm observed a flock of 20 in a flooded alfalfa field in Polk County on 30 April 1975.

Spotted Sandpiper (*Actitis macularia*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive in the Western Upland 20–30 April (earliest—2 April 1953, Burnett County) and peak abundance occurs 5–15 May. Peak fall abundance occurs during mid-August and departure by 1 October.

Nesting Season Distribution: Fairly common nesting species throughout the Valley. Nest records and observations of breeding pairs have been obtained from all the counties.

Habitat: Primarily a nesting species of seasonally, semipermanently, and permanently flooded wetlands in the Western Upland and Central Plain. This species also makes extensive use of river edge and exposed islands in larger streams. Largely restricted to rivers, streams, and rocky or sandy shores of large lakes in the Northern Highland.

Ruddy Turnstone (*Arenaria interpres*)

Status: Regular migrant.

Migration: Rare and local migrant throughout the Valley. Spring migrants arrive about 10 May and are most commonly observed 15–25 May. Departure occurs by 5 June (latest—10 June 1972, Burnett County). The observation of 18 ruddy turnstones on Lake Chisago, Chisago County (Roberts 1938), constitutes the largest group reported in the Valley. Fall migrants arrive about 20 August and have departed by 20 September.

Habitat: Ruddy turnstones primarily use sandy beaches associated with large lakes and the shoreline of the St. Croix River. Occasional use is made of seasonally flooded wetlands.

Wilson's Phalarope (*Steganopus tricolor*)

Status: Regular migrant and summer resident, one nest record.

Migration: Fairly common migrant in the Western Upland, locally common in St. Croix County. Rare and local in the Central Plain and Northern Highland. Spring migrants arrive 20–25 April. Peak abundance occurs 10–15 May and departure by 1 June. The first fall migrants arrive 20–30 July. Peak abundance occurs 10–25 August and departure by 15 September.

Nesting Season Distribution: I observed an adult male with at least two young that still retained some down feathers on 10 July 1978 in St. Croix County. The wetland where this brood was observed (Sec. 11, T. 29 N., R. 18 W.) occasionally supports breeding plumaged adults during the nesting season in wet years. Numerous nesting season records from this wetland ranging from 9 June (1964) to 17 July (1961) suggest that nesting may have occurred earlier. Summer records from Crex Meadows, Burnett County (26 June 1974 and 27 June 1972), suggest that Wilson's phalarope may also nest at that location.

Habitat: Wilson's phalaropes use several wetland types during migration, including seasonally and semipermanently flooded wetlands. Summer records are from wetlands where cattail and river bulrush are the predominant vegetation types.

Northern Phalarope (*Lobipes lobatus*)

Status: Regular migrant.

Migration: Rare migrant in the Western Upland and at Crex Meadows, Burnett County. Casual elsewhere. Spring migrants arrive about 10 May (earliest—30 April 1974 and 1 May 1975, St. Croix County). Northern phalaropes are most commonly observed during the third week of May and depart by 5 June. Fall migrants arrive in mid-August (earliest—20 July 1975, St. Croix County) and depart by 15 September.

Habitat: Northern phalaropes are usually observed on semipermanently and permanently flooded wetlands that have poorly developed shoreline or emergent aquatic vegetation.

American Woodcock (*Scolopax minor*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive about 25 March (earliest—14 March 1951, Polk County and 17 March 1955, Burnett County) and peak abundance occurs 20 April to 1 May. Fall migration begins in mid-August. Peak fall abundance occurs 15 September to 1 October and departure by 1 November.

Nesting Season Distribution: Fairly common and well distributed nesting species. Nesting has been recorded in all counties. Surber (1919) made reference to the abundance of this species in Pine County during the early 1900's.

Habitat: American woodcock use a variety of habitats for nesting. In the Western Upland, nesting birds use mesic Southern Deciduous Forest and Lowland Deciduous Forest. In the Central Plain and Northern Highland, open stands of medium-aged aspen and maple forest and Alder Thickets provide optimum nesting habitat. Recently, Deciduous Clear Cuts have been found to provide important nesting habitat.

Common Snipe (*Gallinago gallinago*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Common to locally abundant migrant throughout the Valley. Spring migrants arrive in the Western Upland about 20 March, reaching the Northern Highland about 1 April. Peak abundance during spring migration occurs 20 April to 1 May. Fall migration begins with the flocking of family groups in mid-August. Peak abundance occurs between 25 September and 10 October and departure by 15 November.

Nesting Season Distribution: Uncommon nesting species in the Western Upland, common in the Central Plain and Northern Highland. Confirmed nest records have been obtained from Burnett and Polk counties.

Winter: There are eight late December records ranging from 19 December (1976) to 3 January (1976) in St. Croix and Washington counties. These are all CBC records. The largest count was 12 individuals on the Suburban St. Paul CBC, 30 December 1961. There is only one midwinter record (15 February 1973, Pierce County) for the Valley.

Habitat: Highest densities of nesting common snipe occur in Northern Sedge Meadow. Stream banks and semipermanently flooded wetlands provide important habitat in the Central Plain and Western Upland. In the Northern Highland, breeding common snipe use openings in Black Spruce–Tamarack Bogs and Alder Thicket, in addition to Northern Sedge Meadow.

Short-billed Dowitcher (*Limnodromus griseus*)

Status: Regular migrant.

Migration: Uncommon to rare migrant throughout the Valley. Most records are from the Western Upland and from Crex Meadows, Burnett County. Spring migrants arrive about 10 May and have departed by 30 May. Fall migrants arrive about 25 July (earliest—9 July 1965, St. Croix County) and have departed by 15 September. A short-billed dowitcher that I banded near Roberts, St. Croix County, on 16 August 1975 was recovered in Guyana, South America, in September 1976. Identification of this species and the long-billed dowitcher is compounded by nearly identical plumage characteristics.

Habitat: Largely restricted to flooded alfalfa and stubble fields and borders of seasonally and semipermanently flooded wetlands.

Long-billed Dowitcher (*Limnodromus scolopaceus*)

Status: Regular migrant.

Migration: Uncommon migrant in the Western Upland and Central Plain, rare to absent in the Northern Highland. Spring migrants arrive in the Western Upland 20–25 April and the Northern Highland about 1 May. This species is most frequently observed about 10 May and departs by 15 May. Fall migrants arrive about 10 August (earliest—17 July 1976, St. Croix County). Peak abundance occurs 25 August to 5 September and departure by 5 October (latest—25 and 28 October 1960, St. Croix County; Robbins 1961).

Correct identification of both dowitcher species is difficult because of their similar appearance. To assure positive identification, recognition of their call notes is important. The long-billed dowitcher has a short, two-note "twee twee" call. The short-billed dowitcher call consists of three notes in close succession. This call, "tu-tu-tu," is similar to the greater yellowlegs.

Habitat: Primarily a species of flooded agricultural fields, temporarily, seasonally, and semipermanently flooded wetlands.

Red Knot (*Calidris canutus*)

Status: Casual migrant.

Records: Single red knots were observed in St. Croix County on 12 May 1966 and 13 May 1975. Three birds were observed at Crex Meadows, Burnett County, on 19 May 1972, and single birds on 13 June 1968 and 17 August 1960 (Kemper 1961).

Sanderling (*Calidris alba*)

Status: Regular migrant.

Migration: Rare spring and very rare fall migrant in the Western Upland and at Crex Meadows, Burnett County; absent in the northern forested regions. Spring migrants arrive about 10 May (earliest—30 April 1973, St. Croix County and 2 May 1969, Washington County) and have departed by 30 May. Fall migration is between 15 August and 10 September.

Habitat: Sanderlings are primarily found on sandy or rocky beaches associated with large lakes and sandbars on the St. Croix River. Occasional use is made of drier portions of exposed mud associated with seasonally flooded wetlands and man-made impoundments.

Semipalmated Sandpiper (*Calidris pusillus*)

Status: Regular migrant.

Migration: Common to locally abundant migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Spring migrants arrive about 5 May, reaching peak abundance 15–30 May. Departure occurs 5–10 June (latest—13 June 1965 and 17 June 1977, St. Croix County). Fall migrants arrive about 20 July. Peak abundance occurs 10–20 August and departure by 5 October (latest—16 October 1964; Kemper 1965).

Habitat: Primarily a species of flooded agricultural fields, exposed edges of wetlands, man-made impoundments, and sandbars associated with islands in the St. Croix River.

Western Sandpiper (*Calidris mauri*)

Status: Casual migrant.

Records: There are spring records from St. Croix County including 2–4 May 1975 (peak of 11 on 3 May), 13 May 1976, 25 May 1963, 31 May 1965, and 2 June 1966. There are five fall records including three in St. Croix County; 2 August 1977, 14 August 1975, and 19 August 1974. At Crex Meadows, Burnett County, one western sandpiper was observed on 15 and 21 August 1955, and on 12 October 1974.

Habitat: The St. Croix County observations included birds associated with the exposed edge of a semipermanently flooded wetland. The Burnett County record was obtained from the exposed edge of a man-made impoundment.

Least Sandpiper (*Calidris minutilla*)

Status: Regular migrant.

Migration: Common spring and fairly common fall migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Spring migrants arrive about 30 April (earliest—23 April 1959, Burnett County). Peak abundance occurs 5–15 May and departure by 25 May. Fall migrants arrive 5–10 July (earliest—25 June 1972, Chisago County). Peak abundance occurs 25 July to 10 August and departure by 30 September.

Habitat: Primarily a species of flooded agricultural fields, exposed edges of wetlands, and sandbars associated with St. Croix River islands.

White-rumped Sandpiper (*Calidris fuscicollis*)

Status: Regular migrant.

Migration: Fairly common spring migrant in the Western Upland, uncommon to rare elsewhere. Uncommon to rare throughout the Valley in fall. Spring migrants arrive about 10 May (earliest—20 April 1974, St. Croix County). Peak abundance occurs 20 May to 5 June and departure by 15 June. Fall migrants arrive about 20 July and depart by 15 September (latest—6 October 1964, Kemper 1965). Peak fall populations cannot be determined because of few records.

Habitat: Primarily a species of flooded agricultural fields and muddy edges of seasonally flooded wetlands.

Baird's Sandpiper (*Calidris bairdii*)

Status: Regular migrant.

Migration: Rare spring and uncommon fall migrant in the Western Upland, rare to absent elsewhere. Spring migrants arrive about 5 May (earliest—20 April 1974, St. Croix County) and depart by 5 June. Fall migrants return 15-20 August and depart by 15 September.

Habitat: Primarily a species of temporarily flooded agricultural fields and edges of seasonally flooded wetlands.

Pectoral Sandpiper (*Calidris melanotos*)

Status: Regular migrant.

Migration: Common to locally abundant spring and common fall migrant in the Western Upland and Central Plain, uncommon in the Northern Highland. Spring migrants arrive about 15 April (earliest—4 April 1964 and 1976, St. Croix County) and peak abundance occurs 5-10 May. During this period, flocks of up to 150 individuals are commonly observed. Spring migrants depart by 1 June. Fall migrants return about 10 July, and peak abundance is 15 August to 1 September. Small flocks are observed in early October and departure occurs by 30 October (latest—15 November 1964, Burnett County; Kemper 1965).

Habitat: Pectoral sandpipers use a variety of wetland habitats including temporarily flooded, Northern Sedge Meadow, Shrub Carr, exposed muddy edges of seasonally flooded wetlands and man-made impoundments, and St. Croix River islands.

Dunlin (*Calidris alpina*)

Status: Regular migrant.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive about 5 May, reaching peak abundance 15-20 May. Departure occurs 1-5 June. Fall migrants arrive about 20 August and have departed by 10 October (latest—28 October 1960, St. Croix County).

Habitat: Primarily a species of temporarily and seasonally flooded wetlands, man-made impoundments, and St. Croix River islands.

Stilt Sandpiper (*Micropalama himantopus*)

Status: Regular migrant.

Migration: Rare spring and uncommon fall migrant in the Western Upland, rare to absent elsewhere. Spring migrants arrive about 5 May (earliest—

19 April 1975, St. Croix County). Peak abundance occurs 15–20 May and departure by 25 May. Fall migrants arrive 25 July to 1 August and depart by 25 September.

Habitat: Primarily a species of seasonally flooded wetlands, muddy edges of man-made impoundments, and St. Croix River islands.

Buff-breasted Sandpiper (*Tryngites subruficollis*)

Status: Casual migrant.

Records: There are five records from central St. Croix County: 10 May 1974, 31 July 1967, 11 August 1975, 1 September 1968, and 9 September 1975.

Habitat: All St. Croix County records were obtained from the edge of a semipermanently flooded wetland in Sec. 11, T. 29 N., R. 18 W.

FAMILY STERCORARIIDAE: Jaegers

Parasitic Jaeger (*Stercorarius parasiticus*)

Status: Accidental, two records.

Record: One adult was observed and photographed on 28 and 29 August 1957, on Phantom Lake at the Crex Meadows Wildlife Area, Burnett County (Lound and Lound 1958*a*). D. D. Tessen observed an adult at Crex Meadows on 28 May 1978 (Tessen 1979*a*).

FAMILY LARIDAE: Gulls and Terns

Herring Gull (*Larus argentatus*)

Status: Regular migrant and casual summer resident.

Migration: Common migrant throughout the inland areas, locally abundant along the St. Croix River. Spring migrants return in late February and reach peak abundance 25 March to 20 April. Most have departed by 15 May (latest—25 May 1969, Washington County). Fall migrants arrive during the last 2 weeks of September. Peak abundance occurs 15 October to 1 November and birds depart by 15 December.

Summer: A casual summer resident along the lower St. Croix River. Herring gulls summered in Washington County in 1968 and were observed in Washington County from 14 to 19 July 1975 (Eckert 1976).

Winter: A casual early winter resident in the lower St. Croix River Valley. On 1 January 1972 and 1 January 1975, two herring gulls were observed along the St. Croix River near Hudson (Afton CBC).

Habitat: Largely restricted to larger water bodies, including permanent lakes and the St. Croix River.

Ring-billed Gull (*Larus delawarensis*)

Status: Regular migrant.

Migration: Abundant spring and fall migrant throughout the Valley. Spring migrants return 10–20 March. Peak abundance occurs between 15 April and 1 May and departure by 20 May. Fall migrants arrive in early September (earliest—24 August 1961, Burnett County). Peak abundance occurs between 15 September and 1 October. Flocks totaling 200 individuals are common during this period, and flocks of 500 are regularly observed. Fall migrants depart by 10 November (latest—17 November 1965, St. Croix County and 26 November 1976, Washington County).

Habitat: Ring-billed gulls use a variety of wetland types during migration including semipermanently and permanently flooded wetlands, large lakes, and the St. Croix River. During fall migration, ring-billed gulls make extensive use of recently plowed agricultural fields.

Franklin's Gull (*Larus pipixcan*)

Status: Regular migrant.

Migration: Rare migrant in the Western Upland and at Crex Meadows, Burnett County; absent from the forested regions. Spring migrants arrive between 25 April and 1 May (earliest—13 April 1954, Burnett County) and departure occurs by 25 May. Fall migrants arrive 20–25 September. Peak abundance occurs 1–20 October and departure by 10 November. During peak fall migration, Franklin's gulls are commonly found in association with ring-billed gulls on freshly plowed agricultural fields in western St. Croix County. Flocks of 200 to 300 are not uncommon and during the mid-1960's, S. D. Robbins occasionally found flocks of 1,500 Franklin's gulls in mid-October. Migrants follow a rather narrow migration path through the Western Upland; the major route is associated with the area of Prairie Wetlands. Franklin's gull is virtually absent east of R. 17 W. in St. Croix and Polk counties.

Habitat: Largely restricted to semipermanently and permanently flooded wetlands. Extensive use is made of agricultural fields during fall migration.

Bonaparte's Gull (*Larus philadelphia*)

Status: Regular migrant.

Migration: Uncommon migrant throughout the Valley, fairly common on the prairie wetlands of St. Croix and Washington counties. Spring migrants return between 25 April and 1 May (earliest—12 April 1971, Washington County). Peak abundance occurs 10–15 May and departure by 25 May. Fall migrants arrive about 10 September. Peak abundance occurs 20 September to 1 October and birds depart by 25 October. During the fall, Bonaparte's gulls are most commonly found along the St. Croix River, becoming rare to absent elsewhere.

Habitat: Primarily a species of large semipermanently and permanently flooded wetlands, and open expanses of the St. Croix River.

Ivory Gull (*Pagophila eburnea*)

Status: Hypothetical.

Record: N. R. Stone observed three adults at the Crex Meadows Wildlife Area, Burnett County, on 3 April 1959 (Stone 1959*b*).

Sabine's Gull (*Xema sabini*)

Status: Hypothetical.

Record: A single immature was observed on 1 October 1944 along the St. Croix River at Stillwater, Washington County (Longley 1947).

Common Tern (*Sterna hirundo*)

Status: Regular migrant and casual summer resident.

Migration: Fairly common migrant near the St. Croix River, uncommon to rare elsewhere in the Western Upland and Central Plain, and rare to absent in the Northern Highland. Spring migrants arrive 20–25 April. Peak spring abundance occurs 10–20 May and departure by 30 May. Fall migrants return 25 August to 5 September and depart by 25 September.

Nesting Season Distribution: A casual summer resident in St. Croix and Washington counties; most summering birds are found along the St. Croix River. Establishment of nesting common terns along the lower St. Croix is seemingly possible, because a small group of common terns summer near the confluence of the Minnesota and Mississippi rivers at Ft. Snelling in the Twin Cities. Excessive recreational use of exposed beaches and sandy islands in the lower St. Croix is probably a major factor limiting colony establishment. If colonies are established at a future date, intensive restriction of human use will be necessary.

Habitat: Primarily a species of large permanently flooded wetlands and sandy beaches and islands of the St. Croix River.

Least Tern (*Sterna albifrons*)

Status: Accidental, one record.

Record: R. A. Knuth observed an adult on Phantom Lake, Crex Meadows Wildlife Area, Burnett County, on 17 August 1971 (Roberts and Roberts 1972). This bird was observed by over 60 people during a Wisconsin Society for Ornithology field trip.

Forster's Tern (*Sterna forsteri*)

Status: Regular migrant and casual summer resident. The WDNR listed this species as endangered (Les 1979).

Migration: Fairly common spring and rare fall migrant in the Western Upland and Central Plain, casual in the Northern Highland. Spring migrants arrive 20–25 April and are most commonly observed 5–15 May. Departure of spring migrants occurs by 25 May. Fall migrants arrive between 1–5 September and depart by 1 October.

Summer: A casual summer resident in St. Croix and Washington counties. The presence of summering birds suggests nesting; however, no nests or young have been recorded. This tern occurs with greatest frequency during the summer on the wetlands in St. Croix and Washington counties.

Habitat: Migrants are observed in association with large semipermanently and permanently flooded wetlands. Observations of summering birds have been restricted primarily to permanently flooded wetlands that support extensive growths of cattail and hardstem bulrush along the periphery of the basin.

Caspian Tern (*Sterna caspia*)

Status: Regular migrant.

Migration: Rare migrant in the Western Upland, casual or absent elsewhere. Spring migrants arrive about 1 May (earliest—8 April 1961, Burnett County). Peak abundance occurs 10–20 May and departure by 25 May (latest—30 May 1924, Chisago County; Roberts 1938: 2 June 1974, Washington County; Eckert 1975). Fall migrants arrive about 1 September and have departed by 25 September. During both migration periods, Caspian terns are most regularly observed on the St. Croix River. Away from the river, they are less common and more irregular in occurrence.

Habitat: Largely restricted to open expanses of the St. Croix River and large permanently flooded wetlands.

Black Tern (*Chlidonias niger*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant in the Western Upland and Central Plain; uncommon in the Northern Highland. Spring migrants arrive 25 April to 1 May, reaching peak abundance about 15 May. Fall migrants reach peak numbers about 10 August and have departed by 1 September (latest—4 October 1965, Washington County).

Nesting Season Distribution: A fairly common nesting species in the prairie wetland region of St. Croix, Washington, and southern Polk counties, becoming less common in the forested regions. Breeding populations of the black tern have declined sharply in Wisconsin. During 1966–75, Robbins (1977) noted a 14% annual decrease in the statewide breeding population. A census of breeding black terns in St. Croix County showed a decrease from 42 pairs in 1975 to 9 pairs in 1977 (Faanes 1979).

Habitat: Black terns are a characteristic species of large seasonally and semipermanently flooded wetlands that support an abundance of emergent aquatic vegetation. Most nests that I have examined were on a floating vegetation mat, usually composed of submerged plants and emergent plant leaves. In the northern forested regions, black terns are less common as a nesting species. In this region, large, acidic wetlands are most regularly used for nesting.

FAMILY COLUMBIDAE: Pigeons and Doves

Rock Dove (*Columba livia*)

Status: Regular permanent resident.

Distribution: An abundant permanent resident in cities, towns, and near farm buildings. Uncommon to rare away from human habitation.

Mourning Dove (*Zenaida macroura*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant in the Western Upland and Central Plain, uncommon and more local in the Northern Highland. Spring migrants arrive in mid-March, reaching peak abundance 5–15 April. Fall migration begins with flock formation among immatures in mid-August. Peak abundance occurs between 15 September and 1 October, and most birds depart by 25 October. Several nestlings that I banded in this region were recovered in southern Texas by the end of September during the same year of banding.

Nesting Season Distribution: The mourning dove is an abundant nesting species in the Western Upland and Central Plain. In the Northern Highland, mourning doves are uncommon to rare nesting birds. Mourning doves have a rather long nesting season at this latitude; nest dates range from 18 April to 20 September.

Winter: A fairly common winter resident in the Western Upland, rare to absent elsewhere. The CBC data indicate that the early winter distribution is centered in St. Croix and Washington counties.

Habitat: A characteristic edge species, occurring in largest densities in Pine Plantations, shelterbelts, and fencerows. Occurs fairly commonly in ornamental coniferous trees planted in residential areas.

Passenger Pigeon (*Ectopistes migratorius*)

Status: Extinct.

Records: The destruction of this species across North America has been well documented. Passenger pigeons were a common nesting species in the

Valley until the 1880's. Schorger (1955) described their distribution and cited the last record at New Richmond, St. Croix County, on 28 September 1887. Roberts (1932) mentioned a "pigeon nesting" that was located between White Bear Lake and Taylors Falls in the late 1800's. This location may have been in either Chisago or Washington county.

FAMILY CUCULIDAE: Cuckoos and Anis

Yellow-billed Cuckoo (*Coccyzus americanus*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant in the Western Upland, rare elsewhere. Spring migrants begin to arrive between 15 and 20 May, and become well distributed over the breeding range by 5 June. There is a general exodus of fall migrants 15 August to 10 September, and the last birds depart by 20 September.

Nesting Season Distribution: An uncommon nesting species in Pierce, St. Croix, and Washington counties. Occasional summer records exist for northern Polk and southern Burnett counties. Roberts (1932) mentioned summer records for Pine County and observed that in northern areas this species "seems to vary considerably in numbers, both as to locality and season."

Habitat: A characteristic species of brushy margins, woodlot openings, brushy fencerows, and field edges. Most breeding season adults that I observed were associated with medium-aged stands of Southern Deciduous Forest; red oak and Hill's oak were the predominant vegetation type.

Black-billed Cuckoo (*Coccyzus erythropthalmus*)

Status: Regular migrant and nesting species.

Migration: Uncommon spring and fall migrant throughout the Valley. Spring migrants arrive in the Western Upland between 5 and 10 May, becoming most numerous during the last 2 weeks of May. Night migrants are frequently heard during the first week of June (S. D. Robbins, personal communication). Arrival in the Northern Highland occurs 15–20 May. Peak fall abundance occurs between 1 and 10 September and departure by 25 September.

Nesting Season Distribution: A fairly common nesting species throughout the Valley, although more common in the Central Plain and Northern Highland. Roberts (1938) reported that "a dozen" black-billed cuckoo nests were found during June 1926 in Chisago County.

Habitat: Brushy margins of mature Northern Deciduous Forest, Deciduous Clear Cuts, and mixed coniferous–deciduous forest.

Groove-billed Ani (*Crotophaga sulcirostris*)

Status: Accidental, one record.

Record: One adult was shot in Woodbury Township, Washington County, on 20 October 1968 (Litkey 1969). The specimen was deposited in the museum collection at the University of Wisconsin–River Falls.

FAMILY STRIGIDAE: Typical Owls

Screech Owl (*Otus asio*)

Status: Regular permanent resident.

Distribution: Uncommon permanent resident in the Western Upland and Central Plain, rare to absent elsewhere. Bernard (1967) did not report this species in Douglas County. Green and Janssen (1975) reported that screech owls are resident in Carlton County, indicating possible residence in Pine County. Documented nesting records exist for Pierce, St. Croix, and Washington counties.

Habitat: Breeding screech owls are restricted primarily to mature deciduous forests. Most breeding pairs that I have encountered were associated with Lowland Deciduous Forest that was dominated by cottonwood, American elm, and green ash. In agricultural areas, breeding screech owls are associated with oak woodlots and they are regularly observed using ornamental tree plantings in residential areas.

Great Horned Owl (*Bubo virginianus*)

Status: Regular permanent resident.

Distribution: Common permanent resident throughout the Central Plain and Northern Highland, fairly common (locally common) in the Western Upland. Jackson (1942) reported great horned owls were generally distributed in northwestern Wisconsin.

Habitat: Nesting great horned owls use a variety of habitats, including Lowland Deciduous Forest, mature Northern Hardwood Forest, oak woodlots, Pine Plantations, Lowland Coniferous Forest, and Southern Deciduous Forest.

Long-eared Owl (*Asio otus*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Rare spring and fall migrant throughout the region. Spring migrants arrive 1–15 March and are most commonly seen 20 March to 15 April. Fall migrants arrive about 1 October and most have departed by 1 December.

Nesting Season Distribution: Rare nesting species throughout the Valley. Nesting has been reported in Washington County (Christenson and Fuller 1975). In St. Croix County, the first nest record was obtained near Hudson in 1973, and this pair also produced young in 1974. In Polk County, nesting long-eared owls were found in the McKenzie Creek Wildlife Area (T. 37 N., R. 16 W.) and the Sterling Pine Barrens (T. 36 N., R. 20 W.) during 1972–74. In Burnett County, nests have been found in jack pine habitat west of Grantsburg. Although breeding records are lacking for other counties in the Valley, nesting is expected in suitable habitat.

Winter: Rare winter resident in the Western Upland, casual north of this area.

Habitat: Nesting long-eared owls are usually associated with pine forests and Pine Plantations. The St. Croix County pair was found in a small valley of Southern Deciduous Forest. Wintering long-eared owls are usually associated with Pine Plantations and young pine forests.

Short-eared Owl (*Asio flammeus*)

Status: Regular migrant, casual summer and rare winter resident, one nest record.

Migration: Rare migrant throughout the Valley. Spring migrants arrive about 15 March and are most commonly observed 15–30 April. Most have departed by 10 May. Fall migrants arrive about 25 September. Peak numbers occur 30 October to 1 December and most depart by 15 December.

Nesting Season Distribution: C. R. Elliott observed a short-eared owl nest with three young in St. Croix County on 15 June 1978. This nest was located in a Managed Grassland on the Oakridge Waterfowl Production Area near New Richmond (Sec. 17, T. 31 N., R 17 W.). This represents the only known nest record for the Valley. The presence of additional midsummer records from Crex Meadows, Burnett County (1968–74), Polk County (1974), and St. Croix County (1976) suggest that this species nests sparingly throughout the Valley in suitable habitat. There are no known summer records for the Minnesota counties.

Winter: Rare winter resident in St. Croix, Washington, and Burnett counties. Although most records are from the CBC, two mid-January records exist for Crex Meadows.

Habitat: All breeding season records of this species have been made from Northern Sedge Meadow and retired grassland habitats. Wintering short-eared owls occur in sedge meadows and grassy fields.

Snowy Owl (*Nyctea scandiaca*)

Status: Regular migrant and winter resident.

Migration: Rare spring and fall migrant throughout the Valley. Yearly abundance varies considerably and migrating and wintering populations appear to be regulated by a 4-year cycle of small mammal populations on this species' tundra breeding areas. Fall migrants arrive in mid-November (earliest—14 October 1918, Pine County; 2 November 1963, Crex Meadows) and during "invasion" years, reach peak abundance 15 December to 1 January.

Spring migration begins in late February and departure occurs by 1 April (latest—9 April 1967, Crex Meadows and 18 April 1974, St. Croix County).

Winter: Rare and local winter resident throughout the Valley. During years of peak abundance, snowy owls are fairly common winter residents at Crex Meadows, Burnett County; occasional concentrations range from six to eight birds.

Habitat: Wintering snowy owls regularly use open agricultural fields and Northern Sedge Meadow or Shrub Carr. Occasionally found associated with semipermanently flooded wetlands in the Western Upland and Central Plain. At Crex Meadows, extensive use is made of restored tall grass prairie and Northern Sedge Meadow.

Barred Owl (*Strix varia*)

Status: Regular permanent resident.

Distribution: Fairly common (locally common) in the Central Plain and Northern Highland, common in the Western Upland. There is apparently little difference in status between nesting and winter seasons.

Habitat: Characteristic species of mature Northern Hardwood Forest in the Central Plain and Northern Highland. Predominant vegetation of barred owl habitat includes basswood, sugar maple, trembling aspen, green ash, and white pine. Lowland Coniferous Forest that contains mature yellow birch and black spruce provides important breeding habitat in the Northern Highland. In the Western Upland, the barred owl is characteristic of mature Lowland Deciduous Forest and reaches greatest densities in large expanses of this vegetation type associated with major streams that are tributary to the St. Croix River.

Great Gray Owl (*Strix nebulosa*)

Status: Casual winter resident, one nest record.

Records: One was found dead near Lake Elmo, Washington County, on 15 February 1969 (Green 1969). Another individual was observed at the Northwoods Audubon Center, Pine County, on 27 January 1973. D. G. Follen (personal communication) reported a single great gray owl several times in "early November" 1979, 16 km east of Moose Junction, Douglas County (T. 44 N., R. 13 W.). Follen also reported a great gray owl during November 1979 in extreme northwestern Washburn County, Wisconsin, near the Douglas and Burnett County border.

Nesting Season Distribution: Follen (1979) provided the only evidence of great gray owl nesting in the Valley. On 18 August 1978, he observed two immature great gray owls 0.6 km north of Moose Junction, Douglas County (Sec. 7, T. 44 N., R. 14 W.). The estimated age of these birds was 6–8 weeks. During the observation, an adult was seen and heard nearby. On 19 August 1978, three immatures and one adult were observed at the same location and a stick nest found.

Habitat: Vegetation adjacent to the Douglas County nest was Lowland Coniferous Forest dominated by black spruce, white birch, and green ash. Vast areas of similar habitat exist in southwestern Douglas and adjacent Pine counties. Continued observations in this region may reveal additional breeding records.

Hawk Owl (*Surnia ulula*)

Status: Casual winter resident.

Records: Bernard and Klugow (1963) provided the most evidence of hawk owl occurrence in the Valley. They reported three observations of hawk owls in Douglas County including "one bird 5.6 km north of Dairyland (T. 44 N., R. 14 W.), in early March 1963." On 17 March 1963, a dead hawk owl was found 16 km west of Solon Springs (T. 45 N., R. 13 W.) and on 20 March 1963 another hawk owl (possibly the first individual) was observed 8.8 km northeast of Dairyland. Other records include one bird collected at Stacy, Chisago County, on 20 October 1962, and two birds observed in Pine County on 17 February 1963 (Green 1963).

These observations were made during a winter that produced an "invasion" of hawk owls in northwestern Wisconsin and much of northern Minnesota. Later that same year, the nests and young of two separate pairs were found in northeastern Douglas County. The hawk owl is included as casual rather than accidental, because the species is well known for occasional irruptions into southern areas during the winter (cf. Green 1963; Eckert 1978). Because large expanses of excellent hawk owl habitat (Lowland Coniferous Forest) occur in southern Douglas and adjacent Pine counties, I would expect additional records of this owl during future "invasions."

Boreal Owl (*Aegolius funereus*)

Status: Casual winter resident.

Records: There are two records for Burnett County: 19 December 1952 at Crex Meadows (N. R. Stone), and 13 April 1975 near the Fish Lake Wildlife Area (W. Norling). In Pine County, one was observed on 9 November 1972.

Saw-whet Owl (*Aegolius acadicus*)

Status: Regular migrant and winter resident.

Migration: Rare migrant throughout the Valley. Spring migrants arrive in mid-March, and most observations occur between 25 March and 15 April (latest—16 May 1961, St. Croix County). Fall migrants arrive in mid-September and most have departed by 15 December. This species is one of the least common regular owls in the Valley. At Hawk Ridge near Duluth, Minnesota, saw-whet owls are the most common migrant owl (Evans 1975). No doubt their small size, nocturnal habits, and very secretive behavior contribute to the scarcity of records.

On 24 May 1978, C. A. Kemper and S. D. Robbins heard saw-whet owls calling in four separate locations about 15 km west of Solon Springs, Douglas County. S. D. Robbins (personal communication) suggests that the saw-whet owl probably nests in the upper Valley.

Winter: Apparently a casual winter resident until mid-January. Several late December records exist from the Afton, St. Paul Suburban (Washington County) and New Richmond (St. Croix County) CBC. Also, there are several January records from Burnett County. The recent increased interest in "owling" with tape-recorded calls may help to better establish the winter status of this species.

Habitat: Most records of wintering saw-whet owls have been from medium-aged Pine Plantations and mature pine forests.

FAMILY CAMPRIMULGIDAE: Goatsuckers

Whip-poor-will (*Camprimulgus vociferus*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Western Upland and Central Plain, locally common in the Northern Highland. Most records are of birds on breeding territory, rather than actual migrants. Spring migrants arrive 1–5 May and are widely distributed by 10–20 May. Jackson (1942) reported that whip-poor-wills were common at Danbury, Douglas County, during late May 1918. The status of this species in the fall is poorly understood. Whip-poor-wills are quiet during this period and they are almost never reported. Most observations have been made between 20 August and 20 September (latest—22 October 1964, Burnett County).

Nesting Season Distribution: Fairly common and local nesting species throughout the Central Plain and Northern Highland, uncommon and local in the Western Upland.

Habitat: In the Western Upland, nesting whip-poor-wills are found associated with mixed stands of xeric deciduous and coniferous woods, and in Pine Plantations. In the Central Plain and Northern Highland this species is most common in medium-aged Northern Hardwood Forest, Jack Pine Barren, and Pine Plantations.

Common Nighthawk (*Chordeiles minor*)

Status: Regular migrant and nesting species.

Migration: Common spring and locally abundant fall migrant throughout the Valley. Spring migrants arrive 5–10 May and peak abundance occurs 25 May to 5 June. Fall migration begins with flock formation in early August. Peak abundance occurs between 15 August and 1 September and departure by 20 September (latest—7 October 1973 and 8 October 1965, Washington County).

Nesting Season Distribution: A common nesting species in cities and towns, less common and more localized in areas away from human habitation.

Habitat: This species has adapted well to expanding human population. In cities and towns, an abundance of flat roofs and gravel roadways provide excellent breeding habitat. Although nesting habitat away from human habitation is poorly known, most birds are found associated with mixed deciduous-coniferous forest with sandy soils and open (or barren) understory.

FAMILY APODIDAE: Swifts

Chimney Swift (*Chaetura pelagica*)

Status: Regular migrant and nesting species.

Migration: Chimney swifts are common to locally abundant in the Western Upland and Central Plain, fairly common in the Northern Highland. Because of their relationship with human settlements, this species is most frequently observed near villages and cities. Spring migrants begin to arrive about 30 April and peak abundance occurs 10–20 May. Fall migrants begin to form loose flocks during late July. Peak fall migration occurs between 25 August and 10 September and departure by 20 September (latest—5 October 1947).

Nesting Season Distribution: Breeding chimney swifts have been recorded in all counties of the Valley. Largest breeding populations occur in the Western Upland and Central Plain, where human habitation provides an abundance of nesting sites. Jackson (1942) reported that chimney swifts occurred regularly in the northern regions, even in areas removed from human settlement.

Habitat: Chimney swifts are most numerous in villages and cities where they nest in chimneys and abandoned buildings. Populations of breeding chimney swifts occur in the forested regions where they occupy hollow trees (Jackson 1942) and other natural cavities for nesting.

FAMILY TROCHILIDAE: Hummingbirds

Ruby-throated Hummingbird (*Archilochus colubris*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive during the second week of May (earliest—13 April 1953, Burnett County) and peak abundance occurs 20 May to 1 June. Peak fall abundance occurs 10–25 August and departure by 20 September (latest—1 October 1947, St. Croix County; Robbins 1948*a*).

Nesting Season Distribution: The ruby-throated hummingbird is a fairly common nesting species throughout the Valley; positive or inferred breeding has been recorded in all counties.

Habitat: Breeding ruby-throated hummingbirds occur in a variety of habitat types, most commonly in brushy margins, openings of deciduous forests, and Deciduous Clear Cuts in the Central Plain and Northern Highland. I have found several hummingbird nests in the branches of cottonwoods along the Willow River in St. Croix County. Jackson (1942) noted that in northwestern Wisconsin this species seemed to prefer tamarack bogs for nesting. He speculated that the abundant *Usnea* moss that grows on tamarack was important for nest building.

Rufous Hummingbird (*Selasphorus rufus*)

Status: Accidental, one record.

Record: One rufous hummingbird was observed in Washington County, about 3.2 km west of Prescott, Wisconsin, from the end of September to 15 October 1978 (Binder 1979). This was one of three rufous hummingbirds that occurred in Minnesota during the late summer and fall 1978.

FAMILY ALCEDINIDAE: Kingfishers

Belted Kingfisher (*Megaceryle alcyon*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common migrant throughout the Valley. Apparent increases in populations begin about 1 April and peak abundance occurs 10–25 April. Peak fall migration occurs 10 September to 1 October and most depart by 10 November.

Nesting Season Distribution: The belted kingfisher is a fairly common nesting species throughout the Valley. Probably most abundant in the Central Plain and Northern Highland where there is an abundance of lakes, rivers, and streams.

Winter: An uncommon early winter resident north to Burnett and Pine counties; rare after mid-January. Belted kingfishers are uncommon throughout the winter in Washington, St. Croix, and Pierce counties, where fast-moving streams provide ample open water for fishing.

Habitat: Usually found near permanent lakes and streams that support fish populations. Nests are usually in steep banks adjacent to streams. One nest observed in western St. Croix County was in the bank of a sandstone outcropping about 2 km from the nearest water.

FAMILY PICIDAE: Woodpeckers

Common Flicker (*Colaptes auratus*)

Status: Regular migrant, nesting species, and winter resident.

Table 3. *Mean number of woodpeckers, flycatchers, and swallows recorded on western Wisconsin Breeding Bird Survey transects, 1966–78.*

	Western Upland	Central Plain		Northern Highland	
Species group	Hudson	Dresser	Loraine	Union	Minong
Woodpeckers					
Common flicker	7.1	5.8	7.6	1.9	3.2
Pileated woodpecker	0.0	0.3	1.4	0.8	0.5
Red-bellied woodpecker	0.0	0.6	1.1	0.0	0.0
Red-headed woodpecker	3.4	3.5	3.8	0.5	0.0
Yellow-bellied sapsucker	0.0	0.0	1.4	<0.1	1.1
Hairy woodpecker	1.2	0.6	1.8	1.2	1.0
Downy woodpecker	1.2	0.9	3.3	1.8	1.8
Flycatchers					
Eastern kingbird	5.0	4.9	5.1	4.7	5.0
Great crested flycatcher	6.4	7.2	13.1	19.9	11.0
Eastern phoebe	1.2	0.8	2.4	2.0	2.8
Yellow-bellied flycatcher	0.0	0.0	0.0	0.0	0.1
Willow flycatcher	<0.1	0.0	0.4	0.0	0.0
Alder flycatcher	0.0	0.4	1.2	0.0	4.8
Least flycatcher	<0.1	0.7	5.4	6.0	12.7
Eastern wood pewee	1.9	2.0	6.1	15.4	8.5
Swallows					
Tree swallow	2.4	4.5	8.4	4.7	13.0
Bank swallow	13.8	3.9	6.7	0.0	0.0
Rough-winged swallow	2.7	3.4	3.3	0.0	0.1
Barn swallow	17.3	18.5	18.2	1.2	3.4
Cliff swallow	3.4	4.8	11.5	0.0	8.1
Purple martin	4.7	25.3	11.5	3.2	6.0

Migration: Common to locally abundant migrant throughout the Valley. Noticeable spring movements are observed by 15–25 March. Spring migrants usually travel in small scattered groups; consequently, few large concentrations are observed. Fall migration begins in late August with dispersal of young from the nesting areas. Peak fall migration occurs 15 September to 10 October and most depart by 1 November. During peak movements in fall migration, groups of 40–50 individuals are common, with groups totaling 100 occasionally observed.

Nesting Season Distribution: Breeding Bird Survey data show that the common flicker is the most common and well-distributed breeding woodpecker in the Valley (Table 3). Goddard (1972) found the common flicker the most abundant breeding woodpecker in the Kinnickinnic River Valley, Pierce County. Nesting has been observed in all counties in the Valley.

Winter: Common flickers are rare and local winter residents in the Western Upland and rare or absent in other regions (Table 4). Wintering individuals are occasionally recorded as far north as Burnett and Pine counties.

Table 4. *Relative abundance of various birds on St. Croix River Valley Christmas Bird Counts. Values presented are the mean number of birds per party hour.*

	Western Upland			Northern Highland	
Species groups	Afton	Suburban St. Paul	New Richmond	Grantsburg	Solon Springs
Woodpeckers					
Common flicker	<0.1	<0.1	<0.1	<0.1	0.0
Pileated woodpecker	0.2	<0.1	<0.1	<0.1	<0.1
Red-bellied woodpecker	0.6	0.2	0.2	<0.1	0.0
Red-headed woodpecker	<0.1	<0.1	<0.1	<0.1	0.0
Hairy woodpecker	1.2	0.5	0.3	0.3	0.3
Downy woodpecker	1.8	0.8	0.6	0.4	0.2
Black-backed three-toed woodpecker	0.0	0.0	0.0	0.0	<0.1
Corvids					
Blue jay	6.8	3.1	5.8	3.7	2.7
Common raven	0.0	0.0	0.0	0.1	4.8
Common crow	12.2	3.6	8.1	2.5	0.8
Parids and nuthatches					
Black-capped chickadee	8.0	4.2	2.8	2.1	2.7
Tufted titmouse	0.2	<0.1	0.0	0.0	0.0
White-breasted nuthatch	2.8	1.7	1.0	0.7	0.3
Red-breasted nuthatch	0.1	<0.1	0.0	<0.1	0.3
Selected finches and sparrows					
Cardinal	3.1	0.7	0.8	0.1	0.0
Evening grosbeak	0.5	0.3	0.8	8.3	3.3
Purple finch	2.2	0.4	0.2	<0.1	<0.1
Pine grosbeak	0.2	0.1	0.0	0.2	4.6
Common redpoll	4.5	7.6	6.7	6.8	16.7
Pine siskin	4.0	0.9	0.5	0.7	0.3
American goldfinch	4.1	2.7	3.1	2.3	0.2
Dark-eyed junco	8.9	3.2	2.5	0.2	<0.1
Tree sparrow	6.9	2.0	4.9	0.3	0.0

Habitat: Common flickers are characteristic of the Southern Deciduous Forest, reaching greatest densities in medium-aged oak forest. Fairly common breeding species in Northern Hardwood Forest and Pine Barrens. Uncommon to rare in other habitat types.

Pileated Woodpecker (*Dryocopus pileatus*)

Status: Regular permanent resident.

Distribution: Uncommon to fairly common resident in all regions of the Valley; most numerous along the St. Croix River and its major tributaries. Because of large breeding territories and relative scarcity, low numbers of this woodpecker are recorded along BBS transects (Table 3). All five survey routes traverse fair to good habitat, yet this woodpecker is recorded in very low numbers.

Winter: Winter distribution of this woodpecker is presented in Table 4. Largest winter populations occur in the Western Upland. The pileated woodpecker is fairly regular during winter in Burnett, Douglas, and Pine counties where a combination of Northern Hardwood Forest and coniferous forest provides optimum habitat.

Habitat: The pileated woodpecker is characteristic of large expanses of the mature Lowland Deciduous Forest along and adjacent to the St. Croix River. Fairly common in mature Upland Hardwood Forest and Lowland Coniferous Forest. Uncommon to rare in Southern Deciduous Forest. Rare to absent in other habitat types.

Red-bellied Woodpecker (*Melanerpes carolinus*)

Status: Regular permanent resident.

Distribution: Fairly common breeding bird in the Western Upland, uncommon to rare in the Central Plain, and rare to absent in the Northern Highland. The red-bellied woodpecker is a southern species that reaches its northern range limit along the St. Croix River (Peterson 1951).

Breeding Bird Survey data show that red-bellied woodpeckers occur regularly in central Polk County. Occasional birds with young are observed in Burnett and southern Pine counties. Hamerstrom and Hamerstrom (1963) include two confirmed nest records from along the St. Croix River in western Burnett County. Movement into the northern regions must be fairly recent since Jackson (1942) failed to record this species in 1919 during his work in northwestern Wisconsin. Bernard (1967) considered this species to be very rare in Douglas County, citing three observations in areas north of the St. Croix River. Green and Janssen (1975) cited documented breeding records for Washington County and showed red-bellied woodpecker breeding range extending north to the Chisago–Pine county line.

Winter: Locally a fairly common winter resident in the Western Upland, rare and local adjacent to the St. Croix River in the Central Plain (CBC; Table 4).

Habitat: This woodpecker is a characteristic species of Lowland Deciduous Forest. Large expanses of lowland forest occurring along the St. Croix River and its major tributaries provide excellent breeding habitat. During the breeding season, pairs also use the edge between lowland forest and Southern Deciduous Forest and locally in Northern Hardwood Forest. Wintering birds are found primarily in Lowland Deciduous Forest and Southern Deciduous Forest. This woodpecker is attracted to corncribs on farms near woodland edges during the winter.

Red-headed Woodpecker (*Melanerpes erythrocephalus*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Fairly common spring and fall migrant in the Western Upland and Central Plain. Uncommon and more sporadic in the Northern Highland. The first noticeable influx of spring migrants occurs 20 April to 1 May, reaching peak numbers 15–25 May. Fall migration begins about 10 August in the Northern Highland and 20 August elsewhere. Peak movements occur 20 August to 15 September and most have departed by 1 November.

Nesting Season Distribution: Fairly common breeding species in the Western Upland and Central Plain, rare to uncommon in the Northern Highland. Breeding Bird Survey Data indicate that a uniformly distributed breeding population occurs through the Western Upland and Central Plain (Table 3). Evidence of nesting or the presence of inferred nesting records have been obtained in all counties of the Valley.

Winter: Uncommon and local winter resident in upland oak habitat near the St. Croix River. The CBC data (Table 4) indicate that red-headed woodpeckers occur regularly north to Burnett and Pine counties in winter. Moe (1968) also showed that the winter distribution of red-headed woodpeckers in Wisconsin extended northward including southeastern Burnett County.

Habitat: Breeding red-headed woodpeckers occupy both upland and lowland deciduous forests. Largest breeding densities occur in mature Southern Deciduous Forest in the Western Upland. This woodpecker also uses second growth oak forest and open-oak forest extensively. Mature Lowland Deciduous Forest that is dominated by green ash and American elm is also an important breeding habitat. Suitable breeding habitat is enhanced by the presence of dead or dying trees. The spread of oak-wilt and dutch elm disease has aided in providing additional nesting sites for these birds.

Yellow-bellied Sapsucker (*Sphyrapicus varius*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Uncommon spring and fall migrant in all regions. Spring migrants begin to arrive 25 March to 5 April and peak migration occurs 15 April to 1 May. Fall migration begins 15–25 August. Peak numbers occur 20 September to 5 October and departure by 25 October.

Nesting Season Distribution: Uncommon to fairly common breeding bird in the Northern Highland, uncommon in the Central Plain, rare and local in the Western Upland. Documented nesting records exist for all counties in the Valley.

Winter: Yellow-bellied sapsuckers have been observed twice on the Afton CBC, Washington County: 2 January 1960 and 1 January 1970 (at a feeding station).

Habitat: Yellow-bellied sapsuckers occupy a variety of upland deciduous and coniferous forest types for nesting. This species is most common during the breeding season in climax or near climax Northern Hardwood Forest that is dominated by maple and basswood. Nesting also occurs in mature and second growth aspen–maple forest. Coniferous forests are used to a lesser extent for nesting. Breeding yellow-bellied sapsuckers regularly use extensive stands of Lowland Deciduous Forest in the Western Upland.

Hairy Woodpecker (*Picoides villosus*)

Status: Regular permanent resident.

Distribution: Fairly common breeding bird in the Northern Highland and Central Plain, uncommon and local in the Northern Highland. Goddard (1972) reported a breeding density of 3.45 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County. Breeding Bird Survey data (Table 3) suggest that breeding densities are fairly uniform throughout the Valley.

Winter: Fairly common winter resident in the Western Upland and Central Plain; uncommon in the Northern Upland. The CBC data (Table 4) show the greatest densities occurring along and adjacent to the lower St. Croix River. The largest count was 91 on the Afton CBC, 1 January 1972.

Habitat: Hairy woodpeckers are not indicative of any one habitat type. Breeding pairs occupy a variety of habitats including Lowland Deciduous Forest, Southern Deciduous Forest, Northern Hardwood Forest, and Lowland Coniferous Forest.

Downy Woodpecker (*Picoides pubescens*)

Status: Regular permanent resident.

Distribution: Fairly common in the Western Upland, common in the Central Plain and Northern Highland. Breeding Bird Survey data (Table 3) suggest that the breeding population increases slowly northward across the Valley. Jackson (1942), however, noted that the downy woodpecker was usually less numerous than the hairy woodpecker in northern Wisconsin. Goddard (1972) reported a breeding density of 6.6 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Winter: Common winter resident in the Western Upland, fairly common in the Central Plain and Northern Highland. The mean ratio of downy to hairy woodpeckers in the Valley during winter is 1.5 to 1.0. Only in the Northern Highland does the hairy woodpecker appear to be more numerous than the downy woodpecker. Young (1961) also noted a greater proportion of hairy woodpeckers to downy woodpeckers in northwestern Wisconsin. Largest winter counts were 143 on the Afton CBC, 1 January 1972 and 123 on the Suburban St. Paul CBC, 2 January 1976.

Habitat: Habitat use by the downy woodpecker is characterized by both upland and lowland coniferous and deciduous forests. Edge situations are used more extensively by this species than by the hairy woodpecker, especially for feeding. During winter, downy woodpeckers occupy habitat similar to that used for breeding. In agricultural areas, downy woodpeckers also use corn stubble fields regularly for feeding.

Black-backed Three-toed Woodpecker (*Picoides arcticus*)

Status: Regular migrant, nesting species, and winter resident.

Migration and Winter: Casual fall migrant and winter resident in all regions. Dates for Washington County include 28 October 1964 at Stillwater (Honetschlager 1965), 2 November 1972, and 14 January 1973 (Huber 1974*b*). This woodpecker was observed once in Chisago County on 13 November 1966, and in Pine County on 28 February 1974 (Eckert 1974). Wisconsin records include Polk County, 23 December 1974 at the McKenzie Creek Wildlife Area (T. 37 N., R. 16 W.); Thiel (1978) lists three winter records for Polk County, although he provides no dates or locations. Douglas County records include one bird 9.6 km west of Solon Springs (Sec. 36, T. 45 N., R. 15 W.) on 26 November 1974. One was observed on the Solon Springs CBC on 23 December 1976 (Table 4).

Nesting Season Distribution: Rare and local permanent resident of the Northern Highland. Bernard (1967) considered this woodpecker a "rare permanent resident that nests locally" in Douglas County. The nesting areas that Bernard refers to occur along the Brule River. The only evidence of nesting in the Valley is provided by Knudson (1978). On 3 August 1978, Knudson observed three black-backed three-toed woodpeckers that he considered to be one female and two immatures in T. 43 N., R. 13 W., Douglas County. On 21 or 22 August 1978, Jeffery Knudson observed a male at the same location. Knudson speculated that this was a nesting record.

Habitat: The habitat associated with most black-backed three-toed woodpeckers observed during the breeding season is predominantly Lowland Coniferous Forest. Coniferous trees killed by fire are particularly attractive to this species. Although Knudson (1978) found adult and immature birds using Jack Pine Barrens, this habitat may have been used only as feeding habitat and not for nesting. This species is found in the extensive Lowland Coniferous Forest of Burnett, Douglas, and Pine counties. Additional field work in Lowland Coniferous Forest directly adjacent to the St. Croix River may shed more light on the breeding status of this species.

Northern Three-toed Woodpecker (*Picoides tridactylus*)

Status: Casual winter visitor.

Records: The first bird was observed by K. H. Dueholm on 8 March 1975 in Polk County, and subsequently on 15 March 1975 (Faanes 1975). This bird was using a small Black Spruce–Tamarack Bog (Sec. 12, T. 34 N., R. 16 W.). B. Klugow (personal communication) observed a second northern three-toed woodpecker in Polk County (Sec. 3, T. 33 N., R. 15 W.) on 11 April 1976.

FAMILY TYRANNIDAE: Tyrant Flycatchers

Eastern Kingbird (*Tyrannus tyrannus*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants return to the Western Upland 30 April to 5 May and reach the Northern Highland by 10 May (earliest—11 April 1954, Crex Meadows, Burnett County). Peak spring migration occurs 10–25 May and most birds are on nesting territories by 1 June. Fall migration begins in early August. Peak fall populations occur 20 August to 1 September and departure by 15 September (latest—2 October 1969, Chisago County).

Nesting Season Distribution: Common breeding species in all regions. Confirmed breeding records exist only for Pierce, Polk, and St. Croix counties. Inferred nesting exists for the remaining counties. Breeding Bird Survey data (Table 3) indicate that an unusually uniform and well-distributed breeding population exists within the Valley.

Habitat: Eastern kingbirds use edge habitats probably more than any other flycatcher. Characteristics of typical eastern kingbird breeding habitat include woodlots, scattered clumps of tall shrubs, fencelines, open fields, and edges of sedge meadows. Fences and transmission lines are apparently important components of breeding habitat and are used extensively as hunting perches. Jackson (1942) found eastern kingbirds "especially abundant" in Jack Pine Barrens and regrown burned areas in northwestern Wisconsin.

Western Kingbird (*Tyrannus verticalis*)

Status: Casual migrant and nesting species.

Migration: Rare spring and fall migrant. Records are too few to determine average dates of arrival or departure. However, most observations occur 15 May to 1 September. Migrants have been recorded from Burnett, St. Croix, and Washington counties.

Nesting Season Distribution: Rare nesting species in St. Croix County. Nesting was first reported in 1961 when a pair was successful at Hudson. A pair returned to the same site each year until 1971 when small boys shot the pair from the nest. During the summer of 1967, Peter Tweet found an additional breeding pair near Burkhardt, in west central St. Croix County. Additional breeding season records include a single bird at Crex Meadows, Burnett County, on 27 July 1953, 11 and 26 July, and 5 August 1956. In Minnesota, two young were observed at Langdon, Washington County, on 13 August 1952 (Lupient 1952). In St. Croix County, western kingbirds were not recorded again until I observed a group of four near New Richmond on 16 August 1975. This group remained in the same area until 25 August. The next record was obtained on 19 August 1976, when a single bird was found in the same area. This individual remained in the area until 26 August 1976.

Habitat: The Hudson breeding pair was located in a residential area. Other records of breeding pairs are associated with edge habitats in agricultural areas.

Great Crested Flycatcher (*Myiarchus crinitus*)

Status: Regular migrant and nesting species.

Migration: Uncommon to fairly common migrant throughout the Valley, locally common along the lower reaches of the St. Croix River. Spring migrants generally arrive about 1 May in the Western Upland and 5–10 May in the Northern Highland. Peak abundance occurs 15–30 May. Fall migration begins in mid-August, reaching peak abundance by 1 September. Migrants have departed the Northern Highland by 15 September and the remainder of the region by 25 September.

Nesting Season Distribution: Uncommon nesting species in the Western Upland and Central Plain, fairly common to locally common in the Northern Highland. Breeding Bird Survey data (Table 3) suggest a gradual increase in breeding densities moving northward through the Valley. However, Jackson (1942) recorded great crested flycatchers as "never more than two seen at a locality . . ." in the Northern Highland. Goddard (1972) found this flycatcher to be among the 12 most numerous breeding birds along the Kinnickinnic River Valley in Pierce County. Nesting has been confirmed only in St. Croix County where I observed a nest along the Willow River on 10 June 1975. Although only one nest has been confirmed, inferred nesting records have been obtained in the remaining counties.

Habitat: The great crested flycatcher is a forest species, generally assocaited with the upper canopy of medium-aged to mature deciduous forest. The only confirmed nesting record was obtained from a mature Lowland Deciduous Forest where cottonwood was the predominant tree species. Pairs are commonly recorded in extensive stands of Northern Hardwood Forest and in Southern Deciduous Forest. Use of residential habitats has also been recorded.

Eastern Phoebe (*Sayornis phoebe*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Eastern phoebes are among the first passerines to return in the spring; the first migrants arrive in the Western Upland 20–25 March. Although most observations consist of pairs on breeding territories, a peak in spring migration is apparent 15–25 April. Fall migration begins in mid-August and peak movements occur 5–15 September. Late departure dates range from 1–5 October in the Northern Highland to 20 October in the Western Upland.

Nesting Season Distribution: Fairly common nesting species in all regions and documented nesting records exist from each county. Breeding Bird Survey data (Table 3) indicate a fairly evenly distributed breeding population. Jackson (1942) considered the eastern phoebe to be a very common breeding bird along the St. Croix River. Goddard (1972) reported a density of 9.1 breeding pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: Eastern phoebes are attracted to a variety of edge situations, primarily woods–field border and streamside habitats. During the nesting season, eastern phoebes are usually associated with bridges, culverts, or other man-made structures, sheer cliffs, and rocky outcroppings.

Yellow-bellied Flycatcher (*Empidonax flaviventris*)

Status: Regular migrant, one nesting record.

Migration: Uncommon spring migrant in the Western Upland and Central Plain, locally common in the Northern Highland. Fairly common to locally common fall migrant in all regions. Earliest spring migrants arrive 10–15 May, reaching the Northern Highland about 20 May. Peak migration occurs 20–30 May and departure from most areas by 5 June. Fall migration begins by mid-August (earliest—31 July 1967, Washington County). Peak movements occur 15 August to 1 September and birds depart by 15 September.

Nesting Season Distribution: Bernard (1967) cited the only known nesting record for the region, a nest with four eggs near Wascott (Douglas County) on 21 July 1941. Green and Janssen (1975) cited the observation of singing males near Bruno, Pine County. I observed singing males along the St. Croix River near Gordon, Douglas County, on 20 July 1976, and again on 10 June 1977. In neither instance were nests observed. The yellow-bellied flycatcher is probably more widespread as a nesting species than available records indicate because of the vast amount of suitable nesting habitat in the Northern Highland.

Habitat: The 1976 and 1977 records were obtained from an extensive stand of black spruce–tamarack swamp adjacent to the St. Croix River. At other seasons, this flycatcher regularly uses a variety of edge situations.

Acadian Flycatcher (*Empidonax virescens*)

Status: Casual migrant and possible nesting species.

Records: Observations of this bird at the northern limit of its range have been sporadic. Because of their occurrence during normal nesting periods, this species must be considered a possible nesting bird. St. Croix County records include 12 May 1974 at Roberts, and 15 May 1973, 21 June to 5 July 1963, and 22 July 1965 at Hudson. One record exists of this species in the Minnesota Counties. Bratlie (1976) described observations at Franconia, Chisago County, on 8 and 16 June 1976.

Habitat: A species of deciduous forest habitats including Lowland Deciduous Forest and heavily wooded hillsides in mesic Southern Deciduous Forest.

Willow Flycatcher (*Empidonax traillii*)

The decision of the American Ornithologists' Union (AOU 1973) to split the Traill's flycatcher (*Empidonax traillii*) into two separate species created many problems in range delineation. Before that time, both willow and alder flycatchers were recorded as one species, even though song and habitat differences were readily apparent. Fortunately, S. D. Robbins maintained separate records of both species based on song, and from his work it is possible to draw conclusions on the range of these two species in Wisconsin (Robbins 1974*b*). Because this work was not carried out in Minnesota, only generalized distribution can be provided for that State.

Status: Regular nesting species.

Migration: Most records of this species are of breeding pairs on territory. Consequently, dates of first occurrence are nearly impossible to determine. The earliest record I have of a singing willow flycatcher is 20 May 1974 in St. Croix County. This date is near the usual range of 10–20 May for the arrival of most *Empidonax* flycatchers in the Valley. Fall departure probably begins in early August and most birds have left by 15 September. Because nearly all *Empidonax* flycatchers are silent in the fall, few data exist on their migration.

Nesting Season Distribution: Robbins (1974*b*) cited summer records of this species in St. Croix County in 1961–67 and 1970. There are Polk County records in 1965–67 and 1970 and Pierce County records for 1965–78. S. D. Robbins (personal communication) found a singing male willow flycatcher near Fish Lake, Burnett County, on 17 June 1978 and 22 June 1977. I observed male willow flycatchers on territory in Washington County near Stillwater on 6 July 1978. Breeding Bird Survey data were not separable to species until 1975. Consequently, only recent survey data from the Loraine transect in Polk County provide information on relative abundance (Table 3). One nesting record exists for the region. I found a nest with four eggs along Black Brook, Cylon Township, St. Croix County, on 9 July 1978.

Habitat: Willow thickets and Shrub Carr associations are the primary habitats of this bird. The St. Croix County nest was placed in a young black willow located in an extensive Shrub Carr. Observations of singing males are invariably associated with these wetland types.

Alder Flycatcher (*Empidonax alnorum*)

Status: Regular migrant and nesting species.

Migration: Observations of alder flycatchers during spring are usually pairs on presumed breeding territories. Song dates of first observation usually occur 15–20 May in the Western Upland and about 20 May in the Northern Highland. Alder flycatchers are apparently most numerous 20 May to 5 June. Fall migration begins in mid-August, reaching peak numbers 1–10 September. Departure of this species occurs 15–20 September.

Nesting Season Distribution: Fairly common to locally common nesting species north of the Tension Zone. Within this zone of overlap, observations of breeding pairs have been made in southern Washington and northwestern Pierce counties. Breeding Bird Survey data (Table 3) indicate that the largest breeding populations occur north of the Tension Zone. Documented nesting records exist for Polk and Douglas counties. Faanes and Goddard (1976) cited observations of singing males 15–20 June in northern St. Croix County.

Habitat: Alder flycatchers use a greater diversity of habitat types than is used by the preceding species. Nests in Polk County were in Alder Thicket habitat where speckled alder was the predominant shrub species. Elsewhere, breeding pairs have been recorded in Northern Hardwood Forest, Black Spruce–Tamarack Bogs, and Deciduous Clear Cuts.

Least Flycatcher (*Empidonax minimus*)

Status: Regular migrant and nesting species.

Migration: Common to locally abundant migrant in all regions, reaching largest numbers in the Central Plain and Northern Highland. Spring migrants arrive in the Western Upland 1–5 May and the Northern Highland by 10 May. Peak abundance occurs 15 May in the Western Upland to 20 May in the north. Fall migration begins in early August. Peak fall migration occurs 20 August to 1 September in the north and 25 August to 5 September elsewhere. Departure from the Northern Highland occurs 10–15 September and elsewhere by 30 September (latest—5 October 1974, St. Croix County).

Nesting Season Distribution: Common to locally abundant nesting species in all regions. Goddard (1972) reported a breeding density of 8.1 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County. Confirmed nesting records exist only for Polk County; inferred nesting has been documented in all other counties. Breeding Bird Survey data (Table 3) indicate that least flycatcher breeding populations apparently increase in abundance moving northward through the Valley, reaching peak density in the Northern Highland. Jackson (1942) reported that the least flycatcher was the most abundant flycatcher in Polk and Burnett counties.

Habitat: Primarily an edge species; nesting season least flycatchers are usually recorded in a variety of habitat types. Western Upland breeding birds are usually associated with medium-aged Southern Deciduous Forest and mature Lowland Deciduous Forest. Central Plain and Northern Highland birds are typically recorded in mature Northern Hardwood Forest, Deciduous Clear Cut, and mixed coniferous–deciduous forest. In the Jack Pine Barren regions of the Central Plain, breeding pairs are usually associated with deciduous habitats along streams rather than jack pines.

Eastern Wood Pewee (*Contopus virens*)

Status: Regular migrant and nesting species.

Migration: Eastern wood pewees are among the latest arriving flycatchers in this region, usually not observed until after 15 May (earliest—26 April 1974, Burnett County), and peak migration occurs 20–30 May. Fall migration begins about 5 August in the Northern Highland and 15 August elsewhere. Peak migration occurs 20 August to 1 September and departure by 25 September (latest—27 September 1976, Washington County).

Nesting Season Distribution: Fairly common nesting species in all regions of the Valley. Confirmed nesting has been documented in St. Croix and

Douglas counties with inferred nesting elsewhere. Breeding Bird Survey data (Table 3) indicate that a fairly uniform breeding population occurs in the Western Upland and Central Plain. Relative abundance increases markedly north of that zone. Goddard (1972) found this species to be the sixth most abundant breeding bird along the Kinnickinnic River in Pierce County. The mean breeding density in that area was 27.4 pairs per 40 ha.

Habitat: The eastern wood pewee is characteristic of mature deciduous forest. In the Western Upland, breeding pairs are generally associated with mature Lowland Deciduous Forest and occasionally with mature Southern Deciduous Forest. Central Plain and Northern Highland populations are apparently most numerous in mature Northern Hardwood Forest.

Olive-sided Flycatcher (*Nuttallornis borealis*)

Status: Regular migrant and nesting species.

Migration: The olive-sided flycatcher is among the latest arriving songbirds. Average date of spring arrivals in the Western Upland is 16 May and arrivals in the Northern Highland are during 20–25 May. Dates of peak abundance are not provided, primarily because this bird migrates singly or in small groups. Consequently, very few individuals are recorded daily during periods when they would be expected to be numerous. Migrants have usually departed nonbreeding areas by 1 June (latest—11 June 1974, Pierce County). Fall migrants arrive in the Western Upland during early August and become most conspicuous 20–30 August. Departure from northern nesting areas occurs about 5 September and departure elsewhere by 20 September.

Nesting Season Distribution: The only confirmed evidence of nesting is provided by Green and Janssen (1975) who listed a nest record from Sturgeon Lake, Pine County. Considerable inferred breeding evidence exists for northern Burnett and southern Douglas counties where this bird is an uncommon and local summer resident. Although nests have not been observed, extensive stands of black spruce–tamarack habitat along the St. Croix River in Burnett, Douglas, and Pine counties usually support breeding season adults.

Habitat: Olive-sided flycatchers are characteristic of boreal forest habitat during the nesting season. Extensive stands of Lowland Coniferous Forest, combined with an interspersion of open areas of sphagnum moss provide ideal breeding habitat. Also frequently used are white cedar swamps. One factor that characterizes olive-sided flycatcher habitat is the presence of dead snags that are used for feeding and singing perches.

FAMILY ALAUDIDAE: Larks

Horned Lark (*Eremophila alpestris*)

Status: Regular migrant and nesting species, casual winter resident.

Migration: Common to abundant migrant throughout the Valley. The largest numbers occur in open agricultural regions of the Western Upland and Central Plain. Spring migration begins during late January in the south and the first migrants reach Burnett and Pine counties by 15 February. Peak spring migration occurs between 25 February and 25 March. Peak fall migration occurs between 15 October and 10 November and most have departed by 15 December.

Nesting Season Distribution: Horned larks are common nesting birds in the Western Upland and Central Plain, rare and local in the Northern Highland.

Winter: During the winter, horned larks present a perplexing problem in determining whether individuals are early or late migrants or actual winter residents. North of St. Croix Falls, this species is generally absent from mid-December to late January. South of St. Croix Falls, occasional small flocks of 5 to 20 individuals can be found in open areas during this period. I usually consider displaying individuals to be returning summer residents and consider migration to be commencing with the observation of the first large flocks.

Habitat: Horned larks are characteristic of agricultural areas. Breeding densities appear largest in short vegetation associated with domestic hayfields and oat stubble. This species has adapted well to man's increased agricultural production and breeding pairs regularly use bare cultivated fields and various row-crop fields.

FAMILY HIRUNDINIDAE: Swallows

Tree Swallow (*Iridoprocne bicolor*)

Status: Regular migrant and nesting species.

Migration: Abundant migrant in all regions. Spring migrants arrive in the Western Upland 25 March to 5 April and reach the Northern Highland 5–10 April. Peak spring abundance occurs 20–30 April. Fall migration begins in late July with flocking of family groups. Peak fall abundance occurs 15–30 August and departure by 10 October. During peak fall migration, tree swallows are occasionally observed in massive mixed-species flocks near large water bodies. Concentrations of 4,000 to 5,000 individuals are frequently observed along the lower St. Croix River.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, common and more local in the Northern Highland. Breeding Bird Survey data (Table 3) show that tree swallows are uniformly distributed throughout the Valley.

Habitat: Tree swallows nest in loose, semicolonial associations. Breeding pairs are typically associated with water bodies that are normally near small groves of trees (Western Upland and Central Plain) or along northern Forest Bordered Lakes. Extensive use is made of the edge between deciduous forest and natural openings or agricultural fields. Nests are normally located in natural cavities in tree stumps or fence posts and occasionally in holes in stream banks. Tree swallows have benefited by exploiting the large number of eastern bluebird houses that have been placed in agricultural areas and near residential areas.

Bank Swallow (*Riparia riparia*)

Status: Regular migrant and nesting species.

Migration: Common spring and fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–20 April and reach the Northern Highland 20–25 April. Peak abundance occurs between 25 April and 15 May. Fall migration begins during mid-July. Peak abundance through the Valley occurs between 25 July and 5 August, and departure by 5 September.

Nesting Season Distribution: Common nesting species throughout the Western Upland and Central Plain becoming uncommon to rare and local in the Northern Highland. Breeding Bird Survey data (Table 3) show that the breeding distribution of this swallow is restricted primarily to areas that are not heavily forested.

Habitat: Breeding bank swallows are associated with natural banks along rivers, streams, and lakes. Gravel pits and roadside banks that were exposed during highway construction are also heavily used. Colonies are frequently associated with open agricultural areas that are used extensively for foraging.

Rough-winged Swallow (*Stelgidopteryx ruficollis*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland and Central Plain, north to Grantsburg, Burnett County; rare and local elsewhere. Spring migrants arrive 15–25 April and peak abundance occurs 25 April to 5 May. Fall migration begins in late July with gathering of family groups. Peak abundance occurs between 25 July and 10 August and departure by 1 September.

Nesting Season Distribution: Fairly common (locally abundant) breeding species in the Western Upland and Central Plain, rare to absent in heavily forested regions. Breeding Bird Survey data suggest that this species is the least common of the swallows nesting in the Valley. However, Goddard (1972) found rough-winged swallows among the 10 most abundant breeding bird species along the Kinnickinnic River, Pierce County. Average breeding density in that area was 26.5 pairs per 40 ha. This exceptionally high density results from the numerous exposed limestone cliffs along that river, which provide abundant nesting sites.

Habitat: Breeding rough-winged swallows are usually associated with exposed banks along rivers and streams. Particularly important are limestone cliffs along fast-moving streams and rivers in the Western Upland. Occasional use is made of artificial earthen banks and bridges over small streams.

Barn Swallow (*Hirundo rustica*)

Status: Regular migrant and nesting species.

Migration: Common spring and fall migrant throughout the Valley. Spring migrants arrive in the Western Upland during 15–20 April reaching the Northern Highland about 25 April (earliest—11 April 1953, Burnett County). Peak abundance during spring migration occurs 5–10 May. Fall migration begins about 1 August. Peak fall abundance occurs 25 August to 10 September and departure by 10–15 October.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Breeding Bird Survey data (Table 3) suggest that the barn swallow is the most numerous breeding swallow in the Western Upland and Central Plain.

Habitat: Primarily a species of open habitats, usually associated with human habitation. Most nests are found under bridges or on buildings.

Cliff Swallow (*Petrochelidon pyrrhonota*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley, occasionally abundant near the St. Croix River. Spring migrants arrive in the Western Upland 1–5 May and peak abundance occurs 10–20 May. Fall migration begins in mid-August. Peak fall abundance occurs 1–10 September and departure by 25 September (latest—18 October 1974, Pierce County).

Nesting Season Distribution: Fairly common breeding species throughout the Valley. Breeding Bird Survey data (Table 3) suggest that the abundance of the nesting population increases northward across the Valley.

Habitat: Primarily a colonial or semicolonial nesting species, utilizing barns, sheds, and bridges extensively for nest placement. Occasional groups are found nesting in natural settings, including limestone cliffs.

Purple Martin (*Progne subis*)

Status: Regular migrant and nesting species.

Migration: Common to abundant migrant throughout the Valley. Spring migrants arrive 5–10 April and peak abundance occurs 1–10 May. Fall migration begins about 1 August. Peak abundance occurs 25 August to 1 September and departure by 20 September (latest—6 October 1966, Washington County).

Nesting Season Distribution: Common nesting species throughout the Valley. Jackson (1942) referred to the purple martin as "the most generally distributed" among the swallows in northwestern Wisconsin. Breeding Bird Survey data (Table 3) suggest that the largest densities occur in the Central Plain.

Habitat: The purple martin is one of few species benefiting from expanding human population. Colonial martin houses in residential and rural areas have become vitally important to this species.

FAMILY CORVIDAE: Jays, Magpies, and Crows

Gray Jay (*Perisoreus canadensis*)

Status: Casual migrant, winter and summer resident.

Migration: Irregular migrant throughout the Valley. Earliest fall migration records include 17 October 1976 (Washington County), 25 October 1965 (Crex Meadows, Burnett County), and 1 November 1974 (Chisago County). Most fall observations occur 15 November to 15 December. Green (1967) described an invasion of gray jays in northern Minnesota that resulted in several Valley records. Spring observations range from 23 February 1957 to 30 March 1966 and 6 April 1954 (Crex Meadows, Burnett County).

Nesting Season Distribution: W. Norling observed one pair of gray jays in a spruce forest southwest of Moose Junction, Douglas County, on 3 July 1978. On 27 June 1956, A. C. Sprunt observed several gray jays in the Kohler–Peet Wildlife Area, Burnett County (Lound and Lound 1956*b*). Sprunt found this species near Gordon, Douglas County, on 6 July 1956.

Winter: Irregular winter visitor with documented records only from Burnett (1948, 1955, 1957, and 1976), Pierce (January 2, 1976) and Pine (1973 and 1976) counties. During the winter of 1956–57, gray jays were reported as "numerous" near Grantsburg, Burnett County. This species is probably more common during winter months than available data indicate, particularly in the Northern Highland.

Habitat: During migration and winter, gray jays use a variety of habitats including Lowland Coniferous Forest, Northern Hardwood Forest, and Jack Pine Barren. Summer observations have been restricted to extensive areas of Lowland Coniferous Forest.

Blue Jay (*Cyanocitta cristata*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common to locally abundant migrant in all regions. The first migration movements in spring are usually noted about 1–5 April and peak numbers occur 25 April to 10 May. Fall migration begins in mid-August with the formation of loose flocks. Peak movements during fall occur 5–15 September and most migrants have departed the Northern Highland by 15 November.

Nesting Season Distribution: Fairly common breeding species in the Western Upland and Central Plain, common in the Northern Highland. Goddard (1972) found the blue jay to be among the 10 most common breeding birds in mixed deciduous habitat along the Kinnickinnic River, Pierce County. Mean breeding density in that area was 23 pairs per 40 ha. Breeding

Table 5. *Mean number of corvids, parids, wrens, mimids, and thrushes recorded on western Wisconsin Breeding Bird Survey transects, 1966–78.*

	Western Upland	Central Plain		Northern Highland	
Species group	Hudson	Dresser	Loraine	Union	Minong
Corvids					
Blue jay	4.9	9.0	11.2	29.0	19.1
Common raven	0.0	0.0	0.5	<0.1	3.2
Common crow	36.3	30.2	54.7	28.6	29.5
Parids and nuthatches					
Black-capped chickadee	0.4	0.6	2.4	7.0	8.2
White-breasted nuthatch	0.6	1.8	2.2	1.0	0.5
Red-breasted nuthatch	0.0	<0.1	0.0	0.2	0.5
Wrens					
House wren	8.9	10.4	13.3	14.8	9.0
Winter wren	0.0	0.0	0.0	0.0	0.1
Long-billed marsh wren	0.0	0.2	0.2	0.0	0.0
Short-billed marsh wren	2.5	3.7	6.4	0.0	1.3
Mimids					
Gray catbird	5.2	8.8	16.7	8.0	12.4
Brown thrasher	8.4	9.1	5.2	5.9	5.6
Thrushes					
American robin	30.5	46.1	30.6	19.8	26.9
Wood thrush	0.4	0.6	0.7	0.8	2.2
Hermit thrush	0.0	0.0	0.0	1.4	6.1
Veery	<0.1	1.4	11.2	1.2	27.1
Eastern bluebird	2.1	3.8	3.9	6.7	1.8

Bird Survey data (Table 5) demonstrate a gradual increase in abundance northward across the Valley.

Winter: Blue jays are among the few conspicuous members of the winter avifauna in the Valley. Populations vary considerably each winter because of various environmental factors affecting habitat suitability and food supply. Analysis of CBC data (Table 4) indicates that winter populations are largest in the Western Upland region where the predominant habitat is Southern Deciduous Forest. Winter populations in Jack Pine Barrens (Grantsburg CBC) are also high. Lowest winter populations occur in the mixed deciduous–coniferous forest type of the Northern Highland. Largest CBC counts include 597 (2 January 1976) and 485 (2 January 1977) on the Suburban St. Paul CBC, and 509 (1 January 1970) on the Afton CBC.

Habitat: Blue jays use a variety of habitats for nesting, including deciduous and coniferous communities, edge situations, and various ornamental plantings in residential areas. Highest breeding densities occur in northern coniferous communities including Jack Pine Barren and mixed deciduous–coniferous habitats. In the Western Upland, blue jays are common in Southern Deciduous Forest and in remnants of oak savannah. This species appears to be partial to oak forest. During years of poor acorn production, the migration of this species is heavy. In years of high acorn production, large wintering populations occur.

Black-billed Magpie (*Pica pica*)

Status: Casual, two fall records and one hypothetical record.

Records: K. H. Dueholm observed a black-billed magpie at the McKenzie Creek Wildlife Area, Polk County, on 25 October 1973. C. Strehlow observed one in St.Croix County on 12 November 1921 (Milwaukee Public Museum files). Bernard (1967) described a specimen in the University of Wisconsin–Superior bird collection that was "said to have been taken at Solon Springs in the 1930's. Unfortunately, however, no label is attached to the specimen." Roberts (1932) stated that in Minnesota, the black-billed magpie occurs "as far east as Pine and Goodhue counties, both bordering on the Wisconsin line."

Common Raven (*Corvus corax*)

Status: Regular permanent resident.

Migration: Uncommon spring and fall migrant in the Northern Highland and Central Plain, accidental elsewhere. Definite migratory movements begin about 15 October, reaching a peak by 1 December. Spring migration begins in late February with dispersal from winter territories. Most ravens have reached their breeding territories by 1 April.

Nesting Season Distribution: Breeding Bird Survey data suggest that the common raven is a rare breeding bird in the Central Plain and uncommon in the Northern Upland (Table 5). Documented nest records exist only for Burnett and Polk counties. Jackson (1942) failed to record ravens during his research in northwestern Wisconsin in 1919. Bernard (1967) considered common ravens uncommon in summer, but cited no evidence of breeding.

Winter: Fairly common to common winter resident in the Northern Highland, uncommon to fairly common in the Central Plain. The largest concentrations have been recorded near Solon Springs, Douglas County; 192 were recorded on 23 December 1974.

Habitat: Common ravens are not characteristic of any one habitat during the breeding season. The Burnett County nest was found in an oak savannah that was invaded by jack pine. The Polk County nest was in mixed aspen-maple forest. Observations of apparent territorial common ravens indicate an attraction to Northern Hardwood Forest during the nesting season. Large numbers of common ravens are usually associated with garbage dumps during the winter.

Common Crow (*Corvus brachyrhynchos*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Spring migration begins in the Western Upland during mid-February with dispersal from local winter roosts. Numbers of migrants gradually increase, reaching peak numbers 25 March to 10 April. Fall migration begins in late August with flock formation. Peak movements occur 20 September to 15 October and nonwintering birds have departed by 15 November.

Nesting Season Distribution: Common nesting bird in all regions. Breeding Bird Survey data indicate a fairly uniform breeding population throughout the Valley; greatest abundance is in the Central Plain (Table 5). Documented breeding records exist for all eight counties.

Winter: The CBC data (Table 4) show the winter distribution pattern of the common crow. This species is common to locally abundant in the Western Upland, fairly common in the Central Plain, and rare and local in the Northern Highland. The highest winter counts include 959 (1 January 1975), 941 (1 January 1977), and 908 (1 January 1974), all on the Afton CBC.

Habitat: The common crow is primarily an edge species using several woodland habitat types. Common crow breeding habitat is further characterized by the association of agricultural fields or Old Field Community. Also used is Lowland Deciduous Forest and Northern Hardwood Forest. The occurrence of large farming operations and the resultant abundance of waste grains probably enhance the habitats of the Western Upland for wintering common crows.

FAMILY PARIDAE: Titmice

Black-capped Chickadee (*Parus atricapillus*)

Status: Regular permanent resident.

Distribution: Uncommon (locally common) nesting species in the Western Upland, common and more widespread in the Central Plain and Northern Highland. Analysis of BBS data (Table 5) suggests a rapid increase in abundance moving northward from the southern oak forest type of the Western Upland to the mixed deciduous–coniferous forest of the Northern Highland. Goddard (1972) reported a breeding density of 15.1 pairs per 40 ha in mixed habitats along the Kinnickinnic River, Pierce County. Jackson (1943) reported that this species was "only moderately common at most localities" in northwestern Wisconsin. However, he reported it "seemed to be more plentiful . . . at Solon Springs."

Winter: Common and well-distributed winter resident in the Western Upland and Central Plain, uncommon in the Northern Highland. Christmas Bird Count data (Table 4) also suggest that the largest winter densities occur in the southern regions. Mean numbers of black-capped chickadees on the Afton CBC (Western Upland) are nearly three times as large as those on the Solon Springs CBC (Northern Highland). Comparison of CBC and BBS data (Tables 4 and 5) shows that the relative abundance of this species among physiographic regions is reversed between seasons. This is logical considering the periodic influxes of this species into areas south of the breeding range throughout the eastern United States.

Habitat: The black-capped chickadee is rather cosmopolitan in its choice of habitats during the nesting season. Breeding pairs in the Western Upland use Southern Deciduous Forest and Lowland Deciduous Forest most extensively. Habitat use in the Central Plain includes Northern Hardwood Forest, Lowland Deciduous Forest, Black Spruce–Tamarack Bog, and Jack Pine Barren. In the Northern Highland, extensive use is made of Northern Hardwood Forest, primarily stands of medium-aged mixed forest that is dominated by sugar maple, basswood, and scattered white pine. Also important in this region are Lowland Coniferous Forest, Black Spruce–Tamarack Bog, and remnant stands of Upland Coniferous Forest. One important aspect of black-capped chickadee breeding habitat is the presence of natural cavities or dead snags for nest placement. The spread of Dutch Elm disease, primarily in Lowland Deciduous Forest, may benefit this species. Several breeding pairs that I observed in this habitat in the Western Upland were using holes in dead American elm that had been excavated by woodpeckers.

Boreal Chickadee (*Parus hudsonicus*)

Status: Casual winter resident, one summer record.

Winter: Boreal chickadees have been recorded on several CBC's: Afton—29 December 1966 and 1 January 1972; Suburban St. Paul—1 January 1975; Grantsburg—26 December 1976; and Solon Springs—23 December 1976. A single bird was recorded at St. Croix Falls (Polk County) on 3 January 1950, and one individual in Washington County on 30 September 1972.

Nesting Season Distribution: An adult was seen and heard near Solon Springs, Douglas County, on 27 June 1972. Boreal chickadees are not known to nest in northwestern Wisconsin; Bernard (1967) mentioned only winter records from Douglas County. Green and Janssen (1975) showed that the breeding range of this species in Minnesota extended south to central Carlton County.

The midsummer Douglas County record increases the probability that the boreal chickadee nests rarely in the Valley. An abundance of suitable Lowland Coniferous Forest habitat exists along the St. Croix in southern Douglas County and throughout Pine County. Additional field work in this region during the summer may provide confirmation of nesting.

Habitat: Boreal chickadees observed during the winter are usually found at feeding stations. The June 1972 observation was of a single bird in Lowland Coniferous Forest.

Tufted Titmouse (*Parus bicolor*)

Status: Regular permanent resident.

Distribution: Rare and local breeding species restricted primarily to the Western Upland. Establishment of this species in the lower Valley has been very recent. Roberts (1932) rarely found this bird in southeastern Minnesota and then primarily only during the winter months. Currently, the major area of abundance appears to be along the St. Croix River and its major tributaries north to Marine-on-St. Croix (Washington County). Confirmed nest records have been obtained from St. Croix and Washington counties. Edgar (1943) observed tufted titmice feeding their young in Washington County on 25 July 1943, thus providing the first confirmed nest record for Minnesota. Occasional records from central Polk and southern Burnett counties (Bauers 1964), suggest another range extension. Young (1967) summarized the distribution of this species in Wisconsin and reported that the tufted titmouse was concentrated south of the Tension Zone in that State.

Habitat: Primarily a species of mature Lowland Deciduous Forest associated with major tributaries of the St. Croix River. Near Afton State Park (Washington County) and along the Kinnickinnic River (Pierce County), tufted titmice also use stands of medium-aged Southern Deciduous Forest.

FAMILY SITTIDAE: Nuthatches

White-breasted Nuthatch (*Sitta carolinensis*)

Status: Regular permanent resident.

Distribution: Fairly common permanent resident throughout the Valley, decreasing in abundance northward. Breeding Bird Survey data (Table 5) suggest that breeding white-breasted nuthatches occur in largest numbers in the Central Plain, becoming much less numerous in the heavily forested Northern Highland. Bernard (1967), however, considered this species common in Douglas County. Goddard (1972) reported a breeding season density of 14.7 pairs per 40 ha along the Kinnickinnic River, Pierce County.

Winter: Common winter resident in the Western Upland, fairly common in the Central Plain, and uncommon in the Northern Highland. Christmas Bird Count data (Table 4) show a rapid decrease in relative abundance moving northward through the Valley. Densities in birds per party hour are nearly 10 times greater on the Afton Count (Western Upland) than on the Solon Springs Count (Northern Highland).

Habitat: Primarily a species of various deciduous forest communities including Southern Deciduous Forest, Lowland Deciduous Forest, and Northern Hardwood Forest. Rarely encountered during the breeding season in pure coniferous forest. Although nests are frequently placed in coniferous trees (primarily white pine), breeding pairs are usually associated with extensive mixed deciduous–coniferous forest. Breeding pairs regularly use large deciduous trees in residential areas. Residential feeding stations are important during winter.

Red-breasted Nuthatch (*Sitta canadensis*)

Status: Regular migrant, nesting species, and winter resident.

Migration: An irruptive species, usually an uncommon migrant throughout the Valley. During years of peak migration, red-breasted nuthatches are common to locally abundant, primarily in the Northern Highland and Central Plain. In years when this species stages a major population influx, the first migrants may arrive by 15 July and build gradually to a 20 September to 15 October peak. Fall migrants arrive in the Central Plain and Western Upland during late August (earliest—19 August 1970, Washington County). Peak fall abundance occurs 1 October to 15 November. Peak spring migration occurs 15 March to 15 April and most have departed nonbreeding areas by 15 May.

Nesting Season Distribution: Green and Janssen (1975) reported that nests or family groups were observed in Washington County. These authors showed that the breeding range of the red-breasted nuthatch included all three Minnesota counties. There are no known breeding records for the Wisconsin counties. Nesting season adults are rare in the Central Plain and uncommon in the Northern Highland. Breeding Bird Survey data (Table 5) suggest that this nuthatch is uncommon in southern Douglas County and throughout Pine County.

Winter: Uncommon to rare and irregular winter resident in the Western Upland, uncommon in the Central Plain, and fairly common in the Northern Highland (Table 4). The occasional winter irruptions are considered to be related to the failure of the pinecone crop in northern nesting regions. Young's (1965) analysis of winter red-breasted nuthatch distribution in Wisconsin suggests that largest densities occur north of the Tension Zone.

Habitat: During the nesting season, the red-breasted nuthatch is characteristic of Lowland Coniferous Forest that supports black spruce, tamarack, and yellow birch in the overstory. Occasional breeding pairs are also recorded in Black Spruce–Tamarack Bogs, and in Northern Hardwood Forest that exhibits a mixture of coniferous and deciduous tree species. Winter habitat use is similar to that of the nesting season in the Northern Highland and Central Plain. Wintering red-breasted nuthatches in the Western Upland make extensive use of Pine Plantations. Ornamental conifers associated with feeding stations in residential areas also receive use during the winter.

FAMILY CERTHIIDAE: Creepers

Brown Creeper (*Certhia familiaris*)

Status: Regular migrant, winter resident, and probable nesting species.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–20 March, reaching the Northern Highland about 25 March. Peak spring abundance occurs 10–20 April and departure by 10 May (latest—19 May 1966, Washington County). The first fall migrants arrive in the Western Upland 1–10 September. Peak fall abundance occurs 25 September to 25 October and most have departed by 20 November.

Nesting Season Distribution: Uncommon and local resident, restricted primarily to the Northern Highland, although occasionally observed in the Central Plain. There is no direct evidence of nesting in the Valley. I have observed breeding season adults along the upper St. Croix River in Douglas and Pine counties in 1976 and 1977. Although I observed no nests or young, these records suggest possible nesting. Intensive field work in southern Douglas and throughout Pine counties during late May and June may shed additional light on brown creeper breeding status.

Winter: Brown creepers occur throughout the Valley during early winter; observations were made until 23 December in southern Douglas County. During midwinter this species is rare or absent in the Northern Highland and Central Plain, uncommon and local in the Western Upland.

Habitat: My observations of brown creepers during the nesting season have been confined to extensive stands of Northern Hardwood Forest that are dominated by mixed sugar maple, basswood, white birch, trembling aspen, red pine, and white pine. During the winter Lowland Deciduous Forest, dominated by silver maple, American elm, and green ash, is used extensively. Occasional use is also made of mixed-oak forest and Pine Plantations.

FAMILY TROGLODYTIDAE: Wrens

House Wren (*Troglodytes aedon*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 20–25 April (earliest—15 April 1978, St. Croix County) and reach the Northern Highland about 25 April. Peak spring migration occurs 1–10 May. Peak fall migration occurs 25 August to 15 September and departure by 10 October.

Nesting Season Distribution: Breeding Bird Survey data (Table 5) show that this is the most numerous wren in the Valley during the nesting season and that relative abundance is similar throughout the Valley. Jackson (1943) observed that the house wren was a common nesting species throughout northwestern Wisconsin. Goddard (1972) found that house wrens were the third most abundant breeding species in the Kinnickinnic River Valley, Pierce County. Mean density in that area was 36.1 pairs per 40 ha.

Habitat: A characteristic species of several deciduous forest communities including Southern Deciduous Forest, Old Field Community, Northern Hardwood Forest, Lowland Deciduous Forest, and Deciduous Clear Cut. Also important are edge habitats including forest–agricultural field borders, brushy road ditches, and brushy fencerows. Jackson (1943) found house wrens "especially abundant" in burns and cut-over land. This species has adapted well to ornamental plantings in residential areas and is a familiar "back yard" bird, responding especially well to artificial cavities.

Winter Wren (*Troglodytes troglodytes*)

Status: Regular migrant and nesting species, two winter records.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive in the Western Upland 30 March to 10 April, reaching the Northern Highland 10–15 April (earliest—27 March 1942, Burnett County; Feeney 1942). Peak spring migration through the Valley occurs 15 April to 1 May and departure from non-nesting areas occurs by 10 May. Fall migration begins in late August and the first migrants arrive in the Western Upland 10–15 September. Peak fall abundance occurs 25 September to 15 October and departure by 1 November.

Nesting Season Distribution: Uncommon nesting species restricted primarily to the Northern Highland (Table 5). Hofslund (1952) reported a nest with four young at Solon Springs, Douglas County. Rare and casual elsewhere during the nesting season. Green and Janssen (1975) mentioned summer records but no broods from Washington County. Several recent records suggest that the winter wren is probably established as a nesting species in northeastern Chisago County. Longley (1973*b*) reported winter wrens along Lawrence Creek, Chisago County, on 9 June 1973, and Bratlie (1976) observed a winter wren nest at the same location on 16 June 1976.

Winter: There are two records (1 January 1968 and 1973) from the St. Croix County portion of the Afton CBC.

Habitat: The winter wren is a characteristic nesting species of Lowland Coniferous Forest dominated by black spruce, balsam fir, and yellow birch. The Chisago County nesting area was described by Longley (1973*b*) as a hardwood forest consisting of sugar maple, yellow birch, American elm, ash, white pine, and red pine.

Bewick's Wren (*Thryomanes bewickii*)

Status: Casual migrant and summer resident.

Records: S. D. Robbins observed Bewick's wrens near North Hudson, St. Croix County, on four occasions: 5–17 May 1963; 13 May 1964; 7 May 1965; and 17 June 1961. Green and Janssen (1975) mentioned that Bewick's wren had been observed during the summer in Washington County.

Carolina Wren (*Thyrothorus ludovicianus*)

Status: Casual migrant, nesting species, and winter visitor.

Migration Records: Roberts (1938) reported the observation of a single Carolina wren at Woodbury, Washington County, on 30 May 1935. One was observed at St. Croix Falls, Polk County (no date), during 1940 (Kumlien and

Hollister 1951). I found one along the Kinnickinnic River, Pierce County, on 26 April 1977. S. D. Robbins found one near Roberts, St. Croix County, on 3 May 1965 (Faanes and Goddard 1976). Olyphant (1972) caught and banded a Carolina wren in Washington County on 26 October 1971. This bird remained in the area through at least 4 January 1972.

Winter: One Carolina wren was reported on the Afton CBC in Washington County on 1 January 1974 (Eckert 1974). W. Gantenbein observed single Carolina wrens at Osceola, Polk County, during December 1965 to 13 January 1966 (Hilsenhoff 1966), and December 1966 to 14 January 1967.

Nesting Season Distribution: Green and Janssen (1975) reported that Carolina wrens have nested in Washington County. In 1938, two Carolina wrens were observed at St. Croix Falls by S. Owen from 15 April to 4 September. During the summer of 1938, several unsuccessful nest searches were made, but on 2 and 3 July the adults were seen with four fully grown young.

Habitat: Primarily a species of Lowland Deciduous Forest and adjacent edge habitats.

Long-billed Marsh Wren (*Cistothorus palustris*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant in the Western Upland and Central Plain, uncommon to rare and local in the Northern Highland. Spring migrants arrive in the Western Upland 25–30 April and the Northern Highland 1–5 May. Peak abundance during spring migration occurs 10–20 May. Fall migration begins in late August. Peak abundance in the Western Upland occurs 5–15 September and departure by 15 October.

Nesting Season Distribution: Uncommon and local nesting species in the Western Upland and Central Plain, rare and local in the Northern Highland. Evidence of nesting has been obtained in Burnett, Chisago, Polk, St. Croix, and Washington counties.

Habitat: A characteristic nesting species of seasonally, semipermanently, and permanently flooded wetlands. Principal vegetation associated with long-billed marsh wren nesting habitat includes cattail, hardstem bulrush, river bulrush, burreed, and phragmites. This species nests in reduced numbers along the edges of more acidic northern Forest Bordered Wetlands and in emergent vegetation along rivers.

Short-billed Marsh Wren (*Cistothorus platensis*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive in the Western Upland 25–30 April and the Northern Highland 1–5 May. Peak spring migration through the Valley occurs 15 May to 5 June. Fall migration begins during early August with a gradual exodus from nesting areas.

Peak fall migration occurs 25 August to 10 September and departure by 1 October.

Nesting Season Distribution: Common to abundant nesting species in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Breeding Bird Survey data (Table 5) suggest that the greatest abundance occurs in the Central Plain.

Habitat: In the Central Plain and Northern Highland, the species is found in Northern Sedge Meadow dominated by tussock sedge, manna grass, and bluejoint grass. In the Western Upland, breeding pairs are frequently encountered in Shrub Carr Wetlands. During dry years, this wren also uses alfalfa and timothy hayfields, Managed Grasslands, and occasionally Old Field Community.

FAMILY MIMIDAE: Mockingbirds and Thrashers

Mockingbird (*Mimus polyglottos*)

Status: Casual visitor.

Records: The first record was obtained at Crex Meadows, Burnett County, on 7 May 1958 (MacBriar 1958). One was recorded at Crex Meadows on 5 and 16 May 1964 (Soulen 1965). Two were recorded in Washington County on 23 May 1978 (Willard 1971) and 19 July 1978 (Green 1979). Single mockingbirds were observed at Crex Meadows on 10 May 1975 and 23 May 1976 (M. Link, personal communication), and on 18 May 1980 (D. D. Tessen, personal communication). Faanes and Goddard (1976) cited a 25 April 1976 record from near Woodville, St. Croix County.

Gray Catbird (*Dumetella carolinensis*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Common (locally abundant) migrant throughout the Valley. Spring migrants arrive in the Western Upland 1–5 May and the Northern Highland 5–10 May. Peak spring abundance occurs 10–20 May. Fall migration begins in mid-August. Peak fall migration occurs 5–20 September and departure 5–10 October.

Nesting Season Distribution: Fairly common (locally common) nesting species in the Western Upland, common in the Central Plain and fairly common in the Northern Highland. Goddard (1972) found the gray catbird the most abundant nesting species in the Kinnickinnic River Valley, Pierce County. Breeding density in that area was 48.9 pairs per 40 ha. Breeding Bird Survey data (Table 5) show that this species is well distributed throughout the Valley and that greatest densities occur in the Central Plain.

Winter: Polk County records include 9 January to 30 March 1956 at Luck (Lound and Lound 1957*a*), and December 1956 to 19 January 1957 (Lound and Lound 1957*b*). A single gray catbird remained at a Newport feeder

(Washington County) until 27 December 1964 (Huber 1965). One observed at St. Croix Falls, Polk County, on 9 March 1948 may have wintered locally (Robbins 1948*c*).

Habitat: Primarily a species of deciduous forest edge habitats. Important among these are second-growth Northern Hardwood Forest, Deciduous Clear Cuts, Old Field Community, and fencerows. Lowland Deciduous Forest is occasionally used in the Western Upland and Black Spruce–Tamarack Bogs receive limited use in the Northern Highland. In residential areas, ornamental shrubbery is used.

Brown Thrasher (*Toxostoma rufum*)

Status: Regular migrant and nesting species, casual early winter resident.

Migration: Common migrant in the Western Upland and Central Plain, fairly common in the Northern Highland. Spring migrants arrive in the Western Upland 20–25 April (earliest—4 April 1975, Washington County) and reach the Northern Highland 25–30 April. Peak spring abundance occurs 1–15 May. Fall migration begins 15–30 August; peak movements occur 5–20 September and departure by 10 October.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, fairly common and more local in the Northern Highland. Jackson (1943) reported this species as "not common" in northwestern Wisconsin in 1919 but almost 50 years later, Bernard (1967) considered brown thrashers "common" in Douglas County. Breeding Bird Survey data (Table 5) suggest a gradual decrease in relative abundance moving northward across the Valley. Major changes in abundance appear to occur between the Central Plain and Northern Highland. Goddard (1972) reported a breeding density of 6.4 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Winter: There are three early winter records from Washington County: 20 December 1969, 29 December 1973, and 1 January 1975. One remained at a Pierce County feeder through 11 January 1976 (Faanes and Goddard 1976).

Habitat: Primarily a species of edge habitats. Important among these are natural clearings in Southern Deciduous Forest, Old Field Community, brushy fencerows, and Deciduous Clear Cuts. Recently logged oak forests and grazed woodlots supporting an abundance of prickly ash and hawthorn are frequently used in the Western Upland.

FAMILY TURDIDAE: Thrushes, Solitaires, and Bluebirds

American Robin (*Turdus migratorius*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant throughout the Valley. The first spring migrants arrive in the Western Upland during the first 10 days of March, reaching the Northern Highland 15–25 March. Peak spring migration through the Valley occurs 25 March to 15 April. Fall migration begins during late August with the formation of loose feeding flocks. Peak fall migration occurs 15 September to 10 October and most have departed by 1 November. During the peak of fall migration, flocks of 50 to 75 individuals are regularly encountered and occasional groups of 200 to 250 have been recorded.

Nesting Season Distribution: Abundant nesting species in the Western Upland and Central Plain, common in the Northern Highland. Jackson (1943) considered the American robin abundant throughout northwestern Wisconsin in 1919. Breeding Bird Survey data (Table 5) show that the American robin is by far the most numerous nesting thrush in the Valley. Goddard (1972) recorded a nesting density of 18.4 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Winter: This species is fairly well distributed throughout the Valley; several midwinter records exist from Burnett, Douglas, and Pine counties. American robins are regularly observed during midwinter in the Western Upland and appear to be dependent on trees and shrubs (mountain ash, cedar) that retain their fruits throughout the period.

Habitat: Breeding American robins are found in nearly all habitat types in the Valley. This species has adapted well to man's continued alteration of the Valley and is a common breeding species in park-like Residential Habitats. The establishment of Pine Plantations, particularly in the Western Upland and Central Plain, has provided increased areas of excellent nesting habitat.

Varied Thrush (*Ixoreus naevius*)

Status: Casual winter visitor.

Records: This western thrush has been recorded in the Valley at least seven times. Minnesota records include one at Stillwater, Washington County, from mid-December to 30 March 1974 (Eckert 1974). Additional Washington County records include single birds on 3 January 1976, late November 1976, and 9 January 1977. Longley (1967) observed a single bird in Chisago County on 13 November 1966. Records from the Wisconsin counties include one bird at Osceola, Polk County, from early December 1948 until 21 April 1949 (Simmons 1949). One apparently wintering bird remained near Grantsburg, Burnett County, from 12 November 1963 to mid-March 1964 (Bauers 1964).

Habitat: Varied thrushes in this region are usually found at feeding stations. Surrounding habitats include Southern Deciduous Forest composed primarily of Hill's and white oak and brushy edges.

Wood Thrush (*Hylocichla mustelina*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive in the Western Upland 1–5 May, reaching the Northern Highland 10–15 May. Peak spring migration through the Valley occurs 10–25 May. During late July this species becomes very secretive and is not regularly encountered. Peak fall migration apparently occurs 15–30 August and departure 20–30 September.

Nesting Season Distribution: Uncommon nesting species throughout the Valley. Jackson (1943) found this species "fairly common" at St. Croix Falls and heard it occasionally at Danbury (Burnett County) in 1919. Breeding Bird Survey data (Table 5) show a fairly uniform breeding density throughout the Western Upland and Central Plain. The greatest abundance apparently occurs in the Northern Highland. In Minnesota, however, Green and Janssen (1975) consider it most common south of the latitude occupied by the Twin Cities. Goddard (1972) reported a density of 2.1 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: In the Western Upland, the wood thrush is most common in mature Southern Deciduous Forest and Lowland Deciduous Forest. Breeding pairs in the Central Plain are most commonly encountered in mesic Northern Hardwood Forest. In the Northern Highland, this species uses Northern Hardwood Forest and is occasionally found in Lowland Coniferous Forest. In all instances, wood thrushes appear to select woodlands with a closed canopy of mature trees.

Hermit Thrush (*Catharus guttatus*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. The hermit thrush is the first of the *Catharus* thrushes to arrive in spring. The first migrants arrive in the Western Upland 5–10 April (earliest—31 March 1967, Washington County) and reach the Northern Highland 10–15 April. Peak spring migration occurs 15–25 April and departure from nonbreeding areas occurs by 10 May. Fall migration begins in late August. Peak abundance occurs 25 September to 15 October and departure by 1 November (latest—5 November 1975).

Nesting Season Distribution: Fairly common nesting species in the Northern Highland, rare and local in the Central Plain (Table 5). Confirmed nest records exist for Douglas and Pine counties, and nesting is inferred in Burnett and Polk counties.

Habitat: This species is characteristic of wet coniferous–deciduous forests in the Northern Highland. Important among these are Lowland Coniferous Forest, Black Spruce–Tamarack Bogs, and low areas of Northern Hardwood Forest. Breeding pairs also use drier portions of Jack Pine Barrens throughout the Northern Highland.

Swainson's Thrush (*Catharus ustulatus*)

Status: Regular migrant and probable nesting species.

Migration: Common spring and abundant fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 5-10 May (earliest—30 April 1950, Polk County), reaching the Northern Highland 10-15 May. Peak abundance through the Valley occurs 15-25 May and departure by 5 June (latest—8 June 1968, Polk County). This species is the first of the *Catharus* thrushes to arrive in the fall. The first migrants arrive in the Western Upland 5-10 August (earliest—27 July 1966, St. Croix County). Peak abundance through the Valley occurs 25 August to 15 September and departure by 10 October.

Nesting Season Distribution: Rare and local in the Northern Highland during the nesting season. There are no confirmed records of nesting in the Valley. Green and Janssen (1975) showed the probable breeding range of this thrush to include northern and central Pine County. Roberts (1932) mentioned records that suggest nesting in Pine County in 1918. I recorded one singing male along the St. Croix River in Douglas County on 20 June 1976. This is my only summer record for the Valley.

Habitat: During migration, Swainson's thrush regularly uses a wide range of deciduous and coniferous communities. My only nesting season record was obtained from a large tract of Lowland Coniferous Forest that was dominated by black spruce, balsam fir, and yellow birch.

Gray-cheeked Thrush (*Catharus minimus*)

Status: Regular migrant.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive in the Western Upland 5-10 May (earliest—1 May 1967, St. Croix County), reaching the Northern Highland about 10 May. Peak migration occurs 15-25 May and departure by 5 June. Fall migrants arrive in the Northern Highland in mid-August, reaching the Western Upland 25-30 August. Peak fall migration occurs 5-15 September and departure by 1 October.

Habitat: Largely restricted to mature tracts of Upland and Lowland Deciduous Forest in the Western Upland. In the Central Plain and Northern Highland, this species is most numerous in Northern Hardwood and Lowland Coniferous Forests.

Veery (*Catharus fuscescens*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 25 April to 1 May, reaching the Northern Highland 1-5 May. Peak spring migration through the Valley occurs 10-25 May. Fall migration begins in early August. Peak abundance occurs 20 August to 10 September and departure by 1 October.

Nesting Season Distribution: Common nesting species in the Northern Highland and Central Plain, uncommon to rare and local in the Western

Upland. Jackson (1943) reported that the veery was common throughout northwestern Wisconsin. The southern limit of the breeding range is closely associated with the southern limit of maple–basswood forest. This range limit occurs about at the latitude occupied by Marine-on-St. Croix, Washington County. Breeding Bird Survey data (Table 5) suggest a rapid increase in relative abundance moving northward across the Valley.

Habitat: Primarily a species occupying various age classes of moist deciduous forest. In the Northern Highland and Central Plain, this species uses mature stands of Northern Hardwood Forest dominated by sugar maple, basswood, trembling aspen, and white birch. Alder Thicket, Lowland Coniferous Forest, and Black Spruce–Tamarack Bogs are also used in these regions. In the Western Upland, habitat use is almost entirely restricted to mixed maple–oak Forest. Occasional use is made of Shrub Carr wetlands that support an abundant growth of silver willow.

Eastern Bluebird (*Sialia sialis*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Fairly common spring and fall migrant in the Western Upland and Central Plain, more localized in the Northern Highland. Spring migrants arrive in the Western Upland 20–30 March (earliest—12 March 1966, Washington County and 12 March 1977, Pierce County) and the Northern Highland about 1 April. Peak abundance through the Valley occurs 15–30 April. Fall migration begins with the formation of loose family groups in mid-August. Peak fall abundance occurs 15 September to 10 October and departure by 1 November (latest—30 November 1967, Washington County). On 17 October 1964, W. E. Scott observed an estimated 200 eastern bluebirds near St. Croix Falls, Polk County (Kemper 1965).

Nesting Season Distribution: Fairly common nesting species throughout the Valley. Jackson (1943) found this species common in northwestern Wisconsin, especially in recently burned areas. Breeding Bird Survey data (Table 5) suggest that a fairly uniform abundance exists throughout the Western Upland and Central Plain, except in the Jack Pine Barren region along the Union transect, Burnett County.

Concern has been expressed about the status of the eastern bluebird in North America (cf. Arbib 1978) and in Wisconsin (R. L. Hine, personal communication). Some authorities believe that population declines are related to mortality on the wintering grounds, whereas others believe these declines are related to competition for nest sites with other hole-nesting species (e.g., house sparrow). Careful monitoring of the Valley population should be undertaken to determine if declines are occurring.

Winter: One bird was observed at St. Croix Falls, Polk County, on 7 and 8 February 1948. Two birds were observed in Washington County on 20 December 1969. Roberts (1932) mentioned, without details, winter records from Washington County.

Habitat: The eastern bluebird is a characteristic species of edge and open habitats including fencerows, early successional stage deciduous forest, Deciduous Clear Cuts, and openings in grazed woodlots. In the Northern Highland and Central Plain, extensive use is made of Jack Pine Barrens. This is evidenced by the high relative abundance of this species along the Union BBS transect, Burnett County. Local populations, particularly in agricultural areas, can be enhanced by the establishment and monitoring of bluebird houses. Many 4-H Clubs and Future Farmers of America (FFA) chapters have created "Bluebird Trails" that are very beneficial in providing nesting sites.

Townsend's Solitaire (*Myadestes townsendi*)

Status: Accidental.

Records: One Townsend's solitaire was observed at Hudson, St. Croix County, from December 1942 to 10 January 1943 (Scott 1943*a*). Longley (1973*a*) described the observation of a single bird in Chisago County on 27 April 1973.

FAMILY SYLVIIDAE: Gnatcatchers and Kinglets

Blue-gray Gnatcatcher (*Polioptila caerulea*)

Status: Regular migrant and nesting species.

Migration: Uncommon and local migrant restricted primarily to the Western Upland. Spring migrants arrive 1–5 May and are most conspicuous after 15 May. Fall migration apparently begins in late July with dispersal of family groups. This species is most common during the fall 1–15 August and departure occurs by 25 August (latest—6 September 1975, Washington County).

Nesting Season Distribution: Uncommon and local nesting species in the Western Upland. Occasional summer records at St. Croix Falls, Polk County, suggest possible nesting. The observations by Breckenridge (in Roberts 1932) and Maurer (1970) of nests at Marine-on-St. Croix are probably the northernmost documented records in the Valley. Breckenridge reported two adults, but no young, at Taylor's Falls, Chisago County, on 11 August 1938 (Erickson and Upson 1938). The area of greatest abundance is restricted to the lower St. Croix River and its major tributaries from Stillwater, Washington County, south to its confluence with the Mississippi River.

The status of this species as a nesting bird in the Valley is apparently changing. Robbins (1963) suggested that as of 1962 blue-gray gnatcatchers "may not be counted on to be present every year" at Hudson, St. Croix County. Since first observing nesting pairs along the Willow River at Hudson in 1973, the number of pairs on one site has risen from 7 in 1973 to 17 in 1978. Expansion of this species along major St. Croix River tributaries in Wisconsin is also evident. During 1976 and 1977, breeding pairs were located along the Kinnickinnic River near Roberts, St. Croix County (Sec. 11, T. 28 N., R. 18 W.), along the Willow River near Jewett, St. Croix County

(Sec. 4, T. 30 N., R. 17 W.), and along the Apple River near Amery, Polk County (Sec. 8, T. 32 N., R. 17 W.). Expansion along streams that are tributary to the St. Croix River in Washington County has also been observed.

Habitat: Characteristic species of mature tracts of Lowland Deciduous Forest along the St. Croix and its tributaries. Several breeding pairs located along the Lower Kinnickinnic River, Pierce County, in 1976 were using medium-aged Southern Deciduous Forest that was dominated by white oak and Hill's oak. The territories occupied by five pairs in 1976 and seven pairs in 1977 along the Willow River were associated with sapling cottonwood and green ash in the Lowland Forest. Three nests were placed from 2.1 to 6.1 m above the ground in young green ash trees.

Golden-crowned Kinglet (*Regulus satrapa*)

Status: Regular migrant and winter resident.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–25 March, reaching the Northern Highland 25–30 March. Peak abundance through the Valley occurs 5–25 April and departure by 15 May. Green and Janssen (1975) stated that the St. Croix River Valley can be included in this species' breeding range in Minnesota, although there are no breeding records to support this. Fall migrants arrive in the Northern Highland in mid-September, reaching the Western Upland 25 September to 1 October. Peak fall abundance occurs 15 October to 1 November and most have departed by 1 December.

Winter: Uncommon to rare and local winter resident in the Western Upland, casual in the Northern Highland where several late December records have been obtained.

Habitat: During migration and winter, this species is most commonly observed in coniferous communities and occasionally in Lowland Deciduous Forest. Most important among coniferous habitats are Pine Plantations and Lowland Coniferous Forest dominated by black spruce, balsam fir, and hemlock.

Ruby-crowned Kinglet (*Regulus calendula*)

Status: Regular migrant, casual summer and early winter resident.

Migration: Common spring and fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 5–10 April, reaching the Northern Highland by 15 April. Peak abundance occurs 1–10 May and departure by 25 May. A female collected at St. Croix Falls, Polk County, on 22 May 1919, was considered a migrant (Jackson 1943). Fall migrants arrive in the Northern Highland 1–10 September, reaching the Western Upland about 10 September (earliest—23 August 1963, St. Croix County). Peak fall abundance occurs 25 September to 10 October and departure by 30 October.

Nesting Season Distribution: There are no documented nest records in the Valley. Green and Janssen (1975) showed that the breeding range of this species in Minnesota extended south to the northern border of Pine County. On 20 and 21 June 1976, I observed two singing male ruby-crowned kinglets along the St. Croix River in Douglas County (Sec. 24, T. 43 N., R. 14 W.). Although the behavior of these birds suggested nesting, I failed to observe nests or young.

Winter: Casual early winter resident in the Western Upland, usually observed during the CBC period. The latest observations are two birds on the Afton CBC 1 January 1976.

Habitat: During migration, this species uses a wide range of both deciduous and coniferous communities. During these periods, ruby-crowned kinglets appear to prefer brushy communities including Deciduous Clear Cuts. The singing males that I recorded in Douglas County were in an extensive Lowland Coniferous Forest dominated by black spruce, balsam fir, and yellow birch.

FAMILY MOTACILLIDAE: Pipits

Water Pipit (*Anthus spinoletta*)

Status: Regular migrant.

Migration: Uncommon migrant in the Western Upland and Central Plain, rare or absent in the Northern Highland. Spring migrants arrive in the Western Upland 25 April to 5 May. Peak spring abundance through the Valley occurs 10–20 May and departure by 25 May. Fall migrants arrive during mid-September. Peak fall abundance occurs 25 September to 10 October and departure by 25 October.

Habitat: Primary habitat includes seasonally flooded wetlands, agricultural fields, and man-made impoundments that are managed for waterfowl production. During fall migration, this species is especially numerous in recently plowed agricultural fields.

FAMILY BOMBYCILLIDAE: Waxwings

Bohemian Waxwing (*Bombycilla garrulus*)

Status: Casual migrant and winter resident.

Migration: This species is erratic in both distribution and abundance. The highest frequency of occurrence appears to be in the Western Upland. Although fall arrival periods are not regular, small flocks begin to arrive 20 November to 15 December. Spring departure is also irregular; most flocks leave by mid-March (latest—6 April 1970, Washington County).

Winter Distribution: An irregular winter resident throughout the Valley. Observations of Bohemian waxwings during midwinter usually consist of flocks of 15 to 30 birds. Most records have been obtained during the CBC period during the last 2 weeks of December.

Habitat: Most of my observations have involved birds foraging at the edge of deciduous forests or flocks in residential areas. The existence of vegetation that retains its fruit into the winter is important in maintaining this waxwing. Among these plants mountain ash and flowering crab apple, established as ornamentals in residential areas, are most important.

Cedar Waxwing (*Bombycilla cedrorum*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common to abundant spring and fall migrant throughout the Valley. Determination of arrival dates is compounded by the irregular nature of waxwing movements. During years when winter populations are very low, the first noticeable influx of migrants occurs 1–20 May, reaching a peak 1–15 June. When summer populations are low, fall movements occur from mid-August through 30 November and peak abundance usually occurs during late September.

Nesting Season Distribution: Fairly common nesting species throughout the Valley. Jackson (1943) reported that cedar waxwings were common throughout most of northwestern Wisconsin during the 1919 nesting season. Breeding Bird Survey data suggest that the largest population occurs in the Central Plain and Northern Highland. Goddard (1972) reported a density of 9.7 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Winter: Common to abundant winter resident in the Western Upland and Central Plain, uncommon in the Northern Highland. Yearly winter populations are characterized by large fluctuations, probably related to the abundance and availability of a food source. This species, like the Bohemian waxwing, is closely associated with fruit-bearing trees during the winter.

Habitat: Primarily a species of open or semi-open deciduous forest. Important among these habitats are openings in Southern Deciduous Forest, Northern Hardwood Forest, and Deciduous Clear Cuts. Nesting cedar waxwings also use, to a lesser extent, coniferous communities and ornamental shrubbery in residential areas.

FAMILY LANIIDAE: Shrikes

Northern Shrike (*Lanius excubitor*)

Status: Regular migrant and winter resident.

Migration: Uncommon to rare migrant throughout the Valley. The first fall migrants arrive in the Northern Highland 20–30 October, reaching the Western Upland 1–15 November (earliest—22 October 1976, St. Croix County). This species is most frequently encountered 20 November to 10 January. During spring migration, peak numbers occur 1–15 March and departure by 15 April (latest—26 April 1953, Burnett County).

Winter: Rare winter resident throughout the Valley, most regularly observed in the Western Upland and Central Plain.

Habitat: Primarily a species of semi-open natural habitats and agricultural communities during migration and winter. Most northern shrikes are observed perched near the edge of wooded habitats and open fields or along fencerows and highway rights-of-way. The northern shrike is observed infrequently in coniferous habitat including Lowland Coniferous Forest and Black Spruce–Tamarack Bogs.

Loggerhead Shrike (*Lanius ludovicianus*)

Status: Regular migrant and nesting species, accidental in winter.

Migration: Formerly common throughout the Valley, this species is now rare during migration. The spring migration period extends from early April (earliest—27 March 1954, Burnett County) through early May. Fall migration occurs from late August through mid-October (latest—2 November 1972, Burnett County). Caution must be exercised when identifying shrikes during April and October, because their plumage is similar to the northern shrike.

Nesting Season Distribution: Formerly a fairly common breeding species; breeding was documented as far north as Solon Springs in Douglas County. Jackson (1943) noted that "several birds were seen in the open pine barrens five miles south of Solon Springs on 4 August 1919, where two families of full grown young were located." Within the last 15 years, however, the status of the loggerhead shrike during the nesting season has changed. Erdman (1970) summarized the status and distribution of this shrike in Wisconsin, concluding that it was experiencing a statewide decline. Erdman provided information on a nest site near Clayton, Polk County, that is now the northernmost location in the Valley. Loggerhead shrikes were observed in southern Pine County during the 1974 nesting season (Eckert 1974). However, no nests or young were found.

During 1977, I located two nesting pairs that produced five young in St. Croix County. In 1978, five pairs were located in that county, primarily between Roberts and New Richmond. I observed an additional pair during July about 6.4 km south of Lake Elmo, Washington County.

Winter: There are two records of the loggerhead shrike during winter including one bird in Washington County on 1 January 1976. R. E. Faanes observed the other bird hunting near a bird feeder in Hudson, St. Croix County, on 15 February 1978.

Habitat: Primarily a species of edge habitats including fencerows, thorny hedgerows, and brush areas associated with grazed deciduous woodlots. Current clean farming practices, including fencerow removal, may be responsible for some of the decline observed in the breeding population.

FAMILY STURNIDAE: Starlings

Starling (*Sturnus vulgaris*)

Status: Introduced. Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant in the Western Upland and Central Plain, less common in the Northern Highland. Dates of spring arrival are difficult to determine because of wintering individuals. However, large increases in the population occur from late February through 20 March. During fall migration, flocks begin forming in early August and peak movements occur 15 September to 15 October.

Nesting Season Distribution: Abundant nesting species in the Western Upland and Central Plain; uncommon and local in the Northern Highland. The first record of this species in the Valley was obtained from St. Croix County in 1937 (Anonymous 1939). Since that time, the starling population has expanded and the species now breeds throughout the Valley. Breeding Bird Survey data show that largest populations occur in areas heavily settled by humans and where agriculture has expanded. The mean number of starlings recorded along the route of the Dresser BBS (Polk County) is 44.3; however, in the heavily forested region traversed by the Union BBS route (Burnett County), this species was not recorded.

Winter: Common to locally abundant winter resident in the Western Upland, fairly common in the Central Plain, and uncommon to rare or absent in the Northern Highland. During this period, large flocks of starlings are associated with cattle feedlots or barnyards in agricultural areas, and near feedmills and feeder operations in residential areas.

Habitat: Starlings nest in a variety of vegetation types, and in residential buildings, or in nest boxes erected for other species. Starlings have been considered an important factor in the decline of several more desirable species including the red-headed woodpecker and eastern bluebird. Because starlings return to their breeding areas and establish territories earlier than other hole-nesting species, they dominate these nest sites before other migrants return.

FAMILY VIREONIDAE: Vireos

White-eyed Vireo (*Vireo griseus*)

Status: Accidental.

Record: An adult white-eyed vireo was trapped and banded at the Warner Nature Center, Washington County, on 3 May 1977 (Wojahn 1977).

Bell's Vireo (*Vireo bellii*)

Status: Casual migrant and summer resident.

Records: Five records exist during 13 May to 7 September: Polk County, 18 May 1974; Chisago County, 7 September 1968; and St. Croix County, 13 May 1964, 17 June to 21 July 1977, and 3 July 1963. The 1977 St. Croix County record may have been a breeding pair. One male was observed almost daily on territory 5.6 km east of New Richmond. The male was heard singing and appeared to be defending a breeding territory. Attempts to locate a nest or a mated female failed.

Habitat: The 1977 observation was of a bird in second-growth Lowland Deciduous Forest along the Willow River.

Yellow-throated Vireo (*Vireo flavifrons*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Spring migrants arrive in the Western Upland 5–10 May and the Northern Highland 10–15 May and are well distributed 15–25 May. Fall migration begins about 15 August. Peak movements occur 25 August to 10 September and departure 20–25 September.

Nesting Season Distribution: Fairly common nesting species in the Western Upland and Central Plain, uncommon and local in the Northern Highland. Jackson (1943) recorded this species nesting at St. Croix Falls, Polk County; however, he failed to obtain records elsewhere in northwestern Wisconsin. Bernard (1967) considered this vireo an "uncommon to rare summer resident" in Douglas County. Nesting records have been obtained from Solon Springs, which is at the northern limit of their range in Wisconsin. There are several nest records for Chisago and Pine counties, the farthest north at St. Croix State Park, Pine County (Sparkes 1953). Breeding Bird Survey data (Table 6) indicate that the breeding population is fairly uniform throughout the Valley. Goddard reported a density of 2.9 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: A characteristic breeding bird of mature deciduous forests. During the breeding season, this species is most commonly found in Northern Hardwood Forest and Lowland Deciduous Forest. Occasional breeding pairs are recorded in residential habitats and in Lowland Coniferous Forest.

Solitary Vireo (*Vireo solitarius*)

Status: Regular migrant and nesting species.

Migration: Uncommon to fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 1–5 May, reaching the Northern Highland by 10 May. Peak spring migration occurs 10–20 May and departure from nonbreeding areas is by 30 May. Fall migration begins in the Northern Highland in mid-August. The first migrants reach other regions by 25 August. Peak fall migration occurs 10–20 September and departure by 30 September (latest—27 October 1970, Pine County).

Table 6. *Mean number of vireos and warblers recorded on western Wisconsin Breeding Bird Survey transects, 1966–78.*

	Western Upland	Central Plain		Northern Highland	
Species	Hudson	Dresser	Loraine	Union	Minong
Vireos					
Yellow-throated	1.2	1.7	2.8	3.8	2.0
Solitary	0.0	0.0	0.2	0.0	1.2
Red-eyed	3.6	6.6	21.3	16.1	41.2
Warbling	6.1	13.1	10.7	3.8	5.4
Warblers					
Black-and-white	0.0	<0.1	1.3	<0.1	6.9
Blue-winged	<0.1	0.0	0.0	0.0	0.0
Golden-winged	0.0	0.3	5.1	0.0	2.5
Nashville	0.0	<0.1	1.4	1.7	20.2
Yellow	2.5	5.8	21.9	1.6	8.0
Magnolia	0.0	0.0	0.0	0.0	<0.1
Cape May	0.0	0.0	0.0	0.0	<0.1
Yellow-rumped	0.0	0.0	0.0	0.2	1.9
Black-throated green	0.0	0.0	0.0	0.0	0.6
Blackburnian	0.0	0.0	0.0	<0.1	0.2
Chestnut-sided	0.3	0.2	5.2	3.9	29.8
Pine	0.0	0.0	0.3	0.4	3.8
Ovenbird	0.0	0.5	4.7	23.7	19.0
Common yellowthroat	7.9	12.6	36.2	14.6	36.2
Mourning	0.0	<0.1	1.2	<0.1	6.3
Connecticut	0.0	0.0	0.0	1.7	2.7
Canada	0.0	0.0	<0.1	0.0	1.7
American redstart	0.0	0.6	5.2	0.3	7.9

Nesting Season Distribution: Documented evidence of nesting by this vireo exists only for Douglas County, where I observed an adult incubating on 11 June 1977. This bird was found along the St. Croix River about 6.4 km west of Gordon, Wisconsin. Although there is considerable evidence of nesting in Burnett and Pine counties, neither nests or young have been observed. Breeding Bird Survey data (Table 6) also suggest that nesting is primarily restricted to the Northern Highland.

Habitat: Solitary vireos are characteristic of Lowland Coniferous Forest. Vegetation associated with the Douglas County nest site was Lowland Coniferous Forest dominated by black spruce and white cedar adjacent to the St. Croix River. Additional observations within the breeding range occur in similar habitat or in Black Spruce–Tamarack Bogs.

Red-eyed Vireo (*Vireo olivaceus*)

Status: Regular migrant and nesting species.

Migration: Common (locally abundant) migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 May, reaching the Northern Highland by 20 May. The peak of migration occurs 20 May to 5 June. Fall migration begins 20–25 August. Peak abundance occurs 10–15 September and departure by 5 October.

Nesting Season Distribution: Fairly common nesting species in the Western Upland, common to locally abundant in the Central Plain and Northern Highland. Goddard (1972) reported this vireo to be among the 10 most abundant breeding birds in the Kinnickinnic River Valley, Pierce County. Mean density in that area was 25.3 pairs per 40 ha. Analysis of BBS data (Table 6) indicates a gradation in abundance moving northward through the Valley. Documented nesting records exist for Polk, St. Croix, and Washington counties and there is evidence of nesting in the other counties.

Habitat: Red-eyed vireos are largely restricted to various deciduous forest types during migration and the nesting season. Although not characteristic of any one habitat type, their abundance is predictable when compared among geomorphic regions.

In the Western Upland, highest breeding densities occur in mature Lowland Deciduous Forest and mature Southern Deciduous Forest. In the Central Plain, breeding populations are greatest in mature Northern Hardwood Forest dominated by sugar maple and basswood. In the Northern Highland, populations are greatest in aspen forest and mature Northern Hardwood Forest.

Philadelphia Vireo (*Vireo philadelphicus*)

Status: Regular migrant.

Migration: Uncommon to rare migrant throughout the Valley. This is the latest arriving vireo; average first appearance is 15 May in the Western Upland. Migrants arrive in the Northern Highland about 20 May. Observations usually are of single birds or occasionally pairs; therefore, peak migration cannot be determined. Spring departure from the southern regions occurs by 30 May and from the Northern Highland by 5 June. Fall migrants arrive 10–15 September. This species is most frequently encountered 15–25 September and departs from 30 September to 5 October (latest—29 October 1970, Washington County).

Habitat: Philadelphia vireos use a variety of habitat types during migration; however, they are most regularly observed in medium-aged to mature Northern Hardwood Forest.

Warbling Vireo (*Vireo gilvus*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland; fairly common in the Central Plain and Northern Highland. Fairly common fall migrant in the Western Upland, uncommon to rare elsewhere. The mean date of spring arrival in the Western Upland is 8 May (earliest—1 May 1976, St. Croix County) and migrants reach the Northern Highland 10–15 May. Peak migration through the Valley occurs 15–25 May. Fall migration begins 10–15 August. Peak fall migration occurs 20 August to 5 September and departure by 20 September. Peak fall migration in the Western Upland occurs 10–20 September and departure by 1 October.

Nesting Season Distribution: Fairly common to locally common nesting species in the Western Upland and Central Plain, rare to locally uncommon in the Northern Highland. Jackson (1943) considered this vireo to be uncommon when compared with the red-eyed vireo in northwestern Wisconsin. Bernard (1967) described this species as a "regular but generally uncommon summer resident" in Douglas County. Breeding Bird Survey data (Table 6) indicate a fairly constant abundance throughout the Valley. Nesting has been documented in all counties.

Habitat: Characteristic nesting species of mature Lowland Deciduous Forest. Highest breeding densities occur in that habitat and mature Northern Hardwood Forest. Other habitats frequently used include Southern Deciduous Forest, Deciduous Clear Cuts, and Residential Habitats.

FAMILY PARULIDAE: Wood Warblers

Black-and-white Warbler (*Mniotilta varia*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Jackson (1943) reported that the black-and-white warbler was "the most abundant of warblers" during the 1919 spring migration in Polk and Burnett counties. Earliest spring migrants arrive in the Western Upland during the last 5 days of April, reaching the Northern Highland 1–5 May. Peak migration occurs 10–20 May, and nonbreeders depart by 25 May. Fall migration begins in mid-August and birds reach the Western Upland 20–25 August. Peak fall migration occurs 10–20 September, and most have departed by 5 October.

Nesting Season Distribution: Uncommon and local nesting species, most frequently encountered in the Northern Highland. Green and Janssen (1975) indicated the breeding range of this warbler extended into northern Washington County. My Minnesota breeding season records have been obtained only in southern Pine County. Confirmed nesting records exist only for Polk County (12 June 1975). Breeding Bird Survey data (Table 6) suggest a rapid increase in relative abundance moving northeast through the Valley. The 12-year mean number of males recorded on Dresser BBS is <0.1, increasing to 1.3 on the Loraine BBS, and 6.9 on Minong.

Habitat: Territorial males have been recorded in both deciduous and coniferous habitats during the breeding season. In deciduous areas, a preference is shown for mature Northern Deciduous Forest, characterized by extensive stands of maple and basswood. This species apparently prefers Northern

Coniferous Forest, Black Spruce–Tamarack Bog, and white cedar communities.

Prothonotary Warbler (*Protonotaria citrea*)

Status: Regular migrant and nesting species.

Migration: Rare migrant in the Western Upland; one record from the Central Plain (7 May 1966, Chisago County) Observations of this warbler are insufficient to determine patterns of spring and fall migration. Most records appear to be birds on or near potential nesting territories. Spring migrants are usually first recorded 10–15 May (earliest—4 May 1974, Pierce County). Records of fall migrants are even more irregular; the latest is 10 September 1975 (St. Croix County). Most observations of this bird during migration periods have been restricted to areas along and adjacent to the St. Croix River in Pierce, St. Croix, and Washington counties.

Nesting Season Distribution: Very rare nesting species, apparently restricted to the Western Upland. Maurer (1970) briefly described the observation of a nest near Marine-on-St. Croix (Washington County) containing one young on 5 July 1970. On 10 July 1945, 11 male prothonotary warblers were found on territory between Marine-on-St. Croix and Stillwater, and three females were observed feeding near nests (Hubert 1945). On 28 June 1945, a single male was observed along the St. Croix River near Osceola, Polk County. Observations of territorial males along the lower reaches of the Kinnickinnic, Willow, and Apple rivers provide evidence of possible additional breeding records.

Habitat: The prothonotary warbler is restricted almost entirely to large stands of mature Lowland Deciduous Forest dominated by cottonwood, green ash, and American elm. The brief description of the habitat near the nest Maurer observed suggests a mixture of willow and basswood.

Worm-eating Warbler (*Helmitheros vermivorus*)

Status: Casual, three spring records.

Records: S. D. Robbins heard and saw one male along Trout Brook Road near Hudson, St. Croix County, on 18 May 1969 (Faanes and Goddard 1976). Maurer (1969) described the observation of a worm-eating warbler in Washington County on 18 May 1969. I observed one near Trout Brook Road in St. Croix County on 18 May 1980. This species has been recorded with increasing frequency in central Minnesota and southern Wisconsin and may become more regular in the lower reaches of the Valley.

Golden-winged Warbler (*Vermivora chrysoptera*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive in the Western Upland 5–10 May, and reach the Northern Highland about 15 May. Jackson (1943) reported that golden-winged warblers were "common" along the St. Croix River near St. Croix Falls from 21–25 May 1919. One pair was observed copulating on 22 May 1919. This warbler apparently migrates singly, or in small very loose flocks; thus periods of peak spring abundance are difficult to determine. Spring migrants have departed nonbreeding areas in the Western Upland by 30 May. Fall migrants reach the Western Upland about 10 August. Peak fall movements occur 20 August to 5 September. Departure from the Northern Highland occurs by 5 September and elsewhere by 15 September.

Nesting Season Distribution: Uncommon and local breeding bird in the Central Plain and Northern Highland. One nest record from the Western Upland (12 June 1976; River Falls, St. Croix County). Confirmed breeding records exist for St. Croix and Polk counties. Green and Janssen (1975) cited inferred breeding records for Chisago and Pine counties, although the golden-winged warbler was referred to as "quite numerous" in Pine County during the nesting season. One was reported from Washington County on 5 July 1970 (Russell 1970). Breeding Bird Survey data (Table 6) suggest that the center of their breeding range is in the Central Plain.

Habitat: Golden-winged warblers appear to be characteristic of second-growth deciduous forest in early developmental stages. Data from nearby Barron County (Wisconsin) show that largest densities occur in Deciduous Clear Cuts that are less than 10 years old (9 pairs per 40 ha). This density decreases to <0.1 pair per 40 ha in mature aspen–maple woods over 40 years old. Breeding golden-winged warblers also use brushy edges of retired agricultural fields, openings in spruce woods, and occasionally Black Spruce–Tamarack Bogs. Golden-winged warblers apparently avoid jack pine habitat; this warbler has yet to be recorded along the Union BBS route (Burnett County) which traverses extensive stands of jack pine forest.

Blue-winged Warbler (*Vermivora pinus*)

Status: Regular migrant and nesting species.

Migration: Rare migrant in the Western Upland, virtually absent elsewhere. Most observations consist of birds on or near presumed breeding territories. Spring migrants arrive 15–20 May, becoming most conspicuous 25 May to 5 June. One spring record exists for Burnett County, 20 May 1956 (Southern 1960). Breeding birds disperse early from the breeding areas. The latest fall date is 15 September 1975 (St. Croix County).

Nesting Season Distribution: Rare and local breeding bird in the Western Upland. Green and Janssen (1975) provided the only evidence of confirmed breeding for the Valley (Washington County). Breeding season birds are largely restricted to areas along major river systems, including the Kinnickinnic, Willow, and lower St. Croix. The northern limit of blue-winged warbler breeding range in Wisconsin and Minnesota closely approximates the southern limit of its congener, the golden-winged warbler. As with other regions of limited overlap, hybrids of these species have been observed. Manley Olson observed a hybrid referable to "Brewster's warbler" on

31 May 1967 in St. Croix County. Olyphant (1973) banded a Brewster's warbler in Washington County on 13 July 1973.

Habitat: In this region, breeding blue-winged warblers are characteristic of extensive stands of mature Lowland Deciduous Forest. Typical vegetation of their breeding habitat includes cottonwood, American elm, and green ash as dominants. Ground-layer vegetation in many situations is usually wood nettle and various grasses. Along the lower Willow River near Hudson, a small group of breeding blue-winged warblers use a savannah-like association of Hill's oak and little bluestem. Brushy fields with invading saplings or scattered trees are also used.

Tennessee Warbler (*Vermivora peregrina*)

Status: Regular migrant.

Migration: Common migrant throughout the Valley. Mean date of spring arrival in the Western Upland is 4 May (earliest—25 April 1948, Polk County; Robbins 1948*c*). Arrival in the Northern Highland occurs 10–15 May. Peak spring migration through the Valley occurs 10–25 May. Departure of spring migrants in the Western Upland and Central Plain occurs 25–30 May. In the Northern Highland, stragglers can still be found until 10 June. Several mid-June records that suggest possible breeding exist for the Solon Springs area. However, there are no known breeding records of this bird in Wisconsin.

The Tennessee warbler is among the earliest fall migrants of this family, usually arriving in the Northern Highland 15–20 July, reaching the Central Plain and Western Upland 25 July to 1 August. Peak fall migration occurs 20 August to 15 September. This warbler has departed the Northern Highland by 25 September and elsewhere by 5 October (latest—12 October 1961, St. Croix County).

Habitat: Migrant Tennessee warblers regularly use both deciduous and coniferous woods. Perhaps because of its abundance, this warbler is also regularly encountered in residential shrubbery. At the peak of migration, this species congregates in tall trees in residential areas. Six to 10 males per block is not unusual on a peak day. Most mid-June records have been of birds in Northern Hardwood Forest, Lowland Coniferous Forest, and Black Spruce–Tamarack Bogs.

Orange-crowned Warbler (*Vermivora celata*)

Status: Regular migrant.

Migration: Fairly common migrant in the Western Upland and Central Plain, uncommon in the Northern Highland. Spring migrants arrive in the Western Upland 25 April to 1 May (earliest—22 April 1949, Burnett County), reaching the Northern Highland 5–10 May. Peak spring migration occurs 10–20 May and departure by 25 May. Fall migrants arrive 1–5 September. Peak fall migration occurs 20 September to 5 October and departure by 10 October (latest—18 October 1976, St. Croix County).

Habitat: Most observations of orange-crowned warblers have been in deciduous woods of various early successional stages. Occasional individuals have been observed foraging at the edge of cattail marshes, primarily during spring migration.

Nashville Warbler (*Vermivora ruficapilla*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley, locally abundant in coniferous habitats of the Northern Highland. Spring migrants begin to arrive in the Western Upland about 1 May, reaching the Northern Highland 10–15 May. Peak spring migration occurs 10–20 May and departure of nonbreeders by 30 May. Fall migration begins with family dispersal in early August; however, the first obvious migratory movements occur after 10 August. The first fall migrants reach the Western Upland about 20 August (earliest—14 August 1963, St. Croix County). Peak fall migration occurs 1–15 September and departure by 5 October (latest—19 October 1968, Pine County).

Nesting Season Distribution: Common breeding bird throughout the Northern Highland; less common and more localized in the Central Plain. No breeding records exist for the Western Upland. Jackson (1943) referred to the Nashville Warbler as "one of the most plentiful Warblers in summer in most of the region" in 1919. Breeding Bird Survey data (Table 6) demonstrate the rapid increase in relative abundance moving northward from the Central Plain.

Habitat: Breeding Nashville warblers have been recorded in a variety of deciduous and coniferous habitats. Greatest use appears to be in coniferous habitats and of these Black Spruce–Tamarack Bogs are probably the most important.

Northern Parula (*Parula americana*)

Status: Regular migrant and summer resident.

Migration: Rare and local migrant in the Western Upland and Central Plain, uncommon in the Northern Highland. Spring migrants arrive 5–10 May in the Western Upland, reaching the Northern Highland 10–15 May. Because of the low numbers recorded, no peak dates have been determined. Departure from the southern regions occurs by 20 May. Fall migration is diffuse as very few birds were recorded each year. Available data suggest that the main period of migration extends from 20 August to 20 September.

Nesting Season Distribution: Rare and local summer resident of the Northern Highland. Available records suggest the main part of their breeding range lies north of the St. Croix River in Douglas and Pine counties. The only Breeding Bird Survey route in the Valley that has recorded this species is the Minong route in Douglas County.

Habitat: Although confirmed nest records are lacking, this species undoubtedly breeds in the Valley. Northern parula observations during the breeding season consist of birds using Lowland Coniferous Forest dominated by a mixture of white cedar, balsam fir, and black spruce. Also typical of their breeding habitat is *Unsea* moss which is used in nest construction.

Yellow Warbler (*Dendroica petechia*)

Status: Regular migrant and nesting species.

Migration: Common spring migrant in all regions; fairly common during fall. Spring migrants arrive in the Western Upland 1–5 May and reach the Northern Highland by 10 May. Peak spring abundance occurs 10–20 May. Fall migration begins with dispersal from breeding areas in late July. The first large fall movement of yellow warblers occurs 1–5 August. Peak fall movements are noted 10–25 August and departure by 5 September.

Nesting Season Distribution: Common breeding species throughout the region with confirmed breeding records from all counties. Jackson (1943) reported that yellow warblers were uncommon breeding birds at the headwaters of the St. Croix River in 1919. Breeding Bird Survey data (Table 6) suggest that the center of yellow warbler abundance in the Valley is in the Central Plain. Goddard (1972) reported a breeding density of 3.4 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: This warbler appears to use a wide range of habitats, including second-growth deciduous and coniferous woodland, Deciduous Clear Cuts, Black Spruce–Tamarack Bogs, Alder Thicket, Shrub Carr, and edge of various natural basin wetlands. Although seemingly ubiquitous in breeding habitat use, it appears that the yellow warbler demonstrates a strong preference for wetland and wetland-associated habitats.

Magnolia Warbler (*Dendroica magnolia*)

Status: Regular migrant and summer resident.

Migration: Fairly common migrant in all regions. Spring migrants arrive in the Western Upland 5–10 May (earliest—1 May 1969, Washington County) and reach the Northern Highland about 15 May. Peak spring migration occurs 15–25 May but stragglers remain until 1 June. Fall migrants arrive in the Northern Highland 15–20 August and the Western Upland about 20 August (earliest—15 August 1976, Washington County). Peak fall migration occurs 5–20 September and departure by 1 October (latest—21 October 1955, Polk County; Foster 1956).

Nesting Season Distribution: Rare and local summer resident, restricted to the Northern Highland. Several summer records (16 June 1973, 28 June 1974, and 12 June 1977 from along the St. Croix River in Douglas County, and 10 June 1977 along the St. Croix in Pine County) suggest the possibility of nesting. Bernard (1967) considered the magnolia warbler a rare summer resident in Douglas County, but provided no evidence of nests.

Habitat: Migrant magnolia warblers occupy a wide range of both deciduous and coniferous habitats. This species is most frequently encountered during migration in early successional stages of northern upland deciduous forest and in Deciduous Clear Cuts. My observations of this warbler during the breeding season have been confined to extensive stands of Black Spruce–Tamarack Bog. This habitat type appears to be used extensively for nesting within their normal breeding range in northern Minnesota and Wisconsin.

Cape May Warbler (*Dendroica tigrina*)

Status: Regular migrant, one summer record.

Migration: Uncommon to rare migrant in the Western Upland and Central Plain, uncommon to locally common migrant in the Northern Highland. Spring migrants arrive in the Western Upland 5–10 May, reaching the Northern Highland about 15 May. During spring migration, Cape May warblers are most regularly observed 15–25 May and have departed by 1 June. Robbins (1973) provided the only summer record for the Valley, a singing male 1.6 km north of Gordon, Douglas County, on 16 June 1971. Fall migration begins in mid-August with first arrivals in the Central Plain about 20 August. During fall they are regularly encountered from 25 August to 10 September and depart by 25 September (latest—29 September 1965, Washington County).

Habitat: Migrant Cape May warblers use various age classes of coniferous habitats and early successional stage deciduous habitats. In residential areas, this species is also attracted to blossoming apple trees and ornamental spruces. Robbins (1973) described the habitat of a group of nesting Cape May warblers along the Brule River as black spruce. The area that Robbins described is 8.0 km north of Solon Springs, Douglas County, and within 4.8 km of the St. Croix River watershed. Because extensive stands of similar black spruce habitat exist along the St. Croix near Solon Springs, I would expect that additional birds could be located. However, to date I have been unsuccessful in finding this warbler during the breeding season along the St. Croix River.

Black-throated Blue Warbler (*Dendroica caerulescens*)

Status: Regular migrant, occasional summer resident.

Migration: Rare migrant throughout the Valley. Most records are from directly adjacent to the St. Croix River. Spring migrants arrive 5–10 May (earliest—2 May 1972, Washington County) and have departed by 25 May. Fall records tend to indicate that this warbler occurs more commonly during that period. Fall migrants arrive 30 August to 5 September. Records indicate that peak fall numbers occur 15–25 September and departure by 30 September (latest—21 October 1961, Polk County).

Nesting Season Distribution: The only evidence of summer residence is provided by Green and Janssen (1975) who reported the most southerly summer records in Minnesota are from "northern Pine County." I have obtained no summer records of this bird within the Valley in Minnesota or Wisconsin. However, during 5–30 June 1971, I regularly observed three pairs of black-throated blue warblers in Bayfield County about 24 km east of Solon Springs. These observations suggest that breeding black-throated blue warblers may also occur in suitable habitat along the northern reaches of the St. Croix River.

Habitat: During migration, this warbler is most common in wet or mesic deciduous forest sites. I have only one record from xeric Southern Deciduous Forest that was dominated by red oak. Observations of black-throated blue warblers during the breeding season in Bayfield County, Wisconsin, were in extensive stands of mature maple–basswood–aspen forest.

Yellow-rumped Warbler (*Dendroica coronata*)

Status: Regular migrant and nesting species, occasional winter resident.

Migration: Abundant migrant throughout the Valley. The yellow-rumped warbler is the most numerous warbler in this region. Spring migrants arrive in the Western Upland about 5 April (earliest—21 March 1975, Pierce County; 24 March 1963, St. Croix County). Migrants reach the Northern Highland 10–15 April. Peak spring migration through the Valley extends from 20 April to 10 May. Departure from nonbreeding areas occurs by 15 May (latest—24 May 1971, Washington County). Fall migration begins in the Northern Highland 15–20 August; however, the first fall migrants do not reach the Western Upland until 10 September. Peak fall migration occurs 20 September to 5 October. Departure from the Northern Highland occurs by 15 October; 1 November is the usual departure date elsewhere. Occasional stragglers remain in the Western Upland through November. Late dates include 30 November 1975, Pierce County and 3 December 1961, St. Croix County.

Nesting Season Distribution: Rare and local breeding bird, restricted primarily to the Northern Highland. Green and Janssen (1975) showed that the breeding range of this warbler extended into northwestern Pine County. Jackson (1943) did not record breeding season yellow-rumped warblers in the Valley during 1919. Breeding Bird Survey data (Table 6) show that a limited number of yellow-rumped warblers occur along the route of the Minong BBS transect in Douglas County.

On 24 June 1974 and 11 June 1977, I recorded singing yellow-rumped warblers along the St. Croix River in Sec. 23, T. 43 N., R. 14 W., Douglas County, and one singing male was recorded along the St. Croix River in Pine County at the U.S. Highway 77 crossing 4.8 km west of Danbury. Singing and behavioral activities suggested nesting, although nests or young were not observed.

Winter: The only record of an overwintering yellow-rumped warbler is that of one bird remaining at a feeder near River Falls, St. Croix County, during the 1960–61 winter (Faanes and Goddard 1976). Two additional early winter records exist from the Afton CBC: 1 January 1970 (St. Croix County) and

1 January 1975 (Washington County). It is not known if these birds remained throughout the winter.

Habitat: During migration, this warbler is ubiquitous, occurring in essentially all available habitats. Breeding season records include birds from extensive stands of Lowland Coniferous Forest, dominated by white spruce, from Black Spruce–Tamarack Bogs, Jack Pine Barren, and areas of mature white pine. Both habitats are used extensively by nesting yellow-rumped warblers within their normal breeding range in northern Minnesota and Wisconsin.

Black-throated Green Warbler (*Dendroica virens*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant throughout the Valley, locally common in the Northern Highland. Spring migrants arrive in the Western Upland 5–10 May, reaching the Northern Highland 10–15 May. Peak spring migration occurs 15–25 May and nonbreeders have departed by 30 May. Fall migration begins in the Northern Highland 15–20 August and the first migrants reach the Western Upland 25–30 August. Peak fall migration occurs 5–20 September and departure by 5 October (latest—7 October 1973, St. Croix County).

Nesting Season Distribution: Uncommon breeding bird in the Northern Highland. Rare and local in southern Pine, Burnett, and northern Polk and Chisago Counties. Jackson (1943) reported this warbler as "not uncommon" at Solon Springs, Douglas County. On BBS transects (Table 6) black-throated green warblers have been recorded only on the Minong route, Douglas County. This warbler was recorded on 9 June 1973 in Chisago County (Longley 1973*b*), but no evidence of nesting was obtained.

Habitat: Mature Northern Hardwood Forest dominated by sugar maple, basswood, and trembling aspen is used extensively. The large expanses of Lowland Coniferous Forest, primarily adjacent to the upper St. Croix River, are also important.

Cerulean Warbler (*Dendroica cerulea*)

Status: Regular migrant and nesting species.

Migration: Rare spring and fall migrant, restricted primarily to the Western Upland and a small region of the Central Plain. Spring migrants begin to arrive 10–15 May. Most observations are after 15 May and are probably of birds on breeding territories. Data are too few to establish fall migration periods. The latest date available is 16 August 1974 in St. Croix County.

Nesting Season Distribution: Rare and local breeding bird. Confirmed nest records exist only for St. Croix County. On 23 June 1976, I observed adults feeding two young in the nest along the Willow River near Hudson (T. 29 N., R. 19 W.). Cerulean warblers occur regularly only in the lower reaches of the Kinnickinnic River (Pierce County) and Willow River (St. Croix County) and near Afton State Park (Washington County). Occasional breeding season records have been obtained at the mouth of the Apple River (St. Croix County) and from lowland forest at Marine-on-St. Croix (Washington County). Records away from the typical range of this warbler in the Valley include two singing males on 2 June 1968 at Franconia, Chisago County, one in Chisago County on 6 June 1971, and one male near Range, Polk County, on 15 June 1968.

Habitat: Breeding season observations of this warbler have been restricted to Lowland Deciduous Forest. Predominant vegetation of these areas include mature stands of American elm, cottonwood, and green ash.

Blackburnian Warbler (*Dendroica fusca*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant in the Western Upland and Central Plain, common in the Northern Highland. Spring migrants arrive 5–10 May, reaching the Northern Highland 10–12 May. Peak spring migration occurs 15–25 May and departure from nonbreeding areas by 30 May. Jackson (1943) considered this warbler "abundant" at St. Croix Falls (Polk County) 21–25 May 1919. Fall migration begins 10–15 August and the first birds reach the Western Upland about 20 August. Peak fall migration occurs 5–15 September and birds depart by 25 September.

Nesting Season Distribution: Uncommon breeding bird, restricted to the Northern Highland. Breeding season records exist for Burnett, Douglas, and Pine counties. The only confirmed nest records are from Pine (Green and Janssen 1975) and Douglas (Chambers 1944) counties. However, it undoubtedly nests elsewhere in the Northern Highland. Jackson (1943) reported that courting Blackburnian warblers were observed at St. Croix Falls on 24 May 1919. He noted that "although no nests were discovered . . . , the environment is favorable for nesting." Breeding Bird Survey data (Table 6) indicate that this bird occurs in relatively low densities during the breeding season in the Northern Highland.

Habitat: The Blackburnian warbler is characteristic of northern coniferous forests. Territorial birds are encountered most regularly in large tracts of Lowland Coniferous Forest dominated by black spruce, white cedar, and hemlock. Breeding birds also use Black Spruce–Tamarack Bogs and white pine forest where remnants still exist.

Chestnut-sided Warbler (*Dendroica pensylvanica*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. The mean date of spring arrival in the Western Upland is 8 May (earliest—2 May 1974, Pierce County) and arrival in the Northern Highland by 12 May. Peak migration occurs 10–25 May and birds have departed nonbreeding areas by 30 May. Fall migration begins in the Northern Highland 5–10 August with dispersal of young, and the first migrants reach the Western Upland 15–20 August. Peak migration occurs 1–15 September. Departure from the Northern Highland occurs 15–20 September and elsewhere by 1 October (latest—5 October 1973, St. Croix County).

Nesting Season Distribution: Common breeding bird in the Northern Highland and that part of the Central Plain north of St. Croix Falls and Taylor's Falls. South of that line, they are uncommon and local, and rare and local in the Western Upland. Green and Janssen (1975) showed that the breeding range of this warbler extended through the three Minnesota counties. On 26 June 1979, I heard and saw territorial males 4.8 km west of Taylor's Falls, Chisago County. Although nests or young were not observed, I have no doubt they nested in this area.

Nests or young have been recorded in all subject Wisconsin counties except Pierce. An area near the Cylon Marsh Wildlife Area (Sec. 15, T. 31 N., R. 16 W.) and at the mouth of the Apple River (Sec. 20, T. 31 N., R. 19 W.), St. Croix County, are the most southerly locations of regular occurrence. Jackson (1943) recorded this warbler only "occasionally" in the Northern Highland near Solon Springs in 1919, but BBS data (Table 6) show that breeding chestnut-sided warblers occur commonly throughout the Valley and that largest densities are in the Northern Highland.

Habitat: Early successional stages of deciduous and coniferous habitats are used for nesting. Deciduous Clear Cuts that are predominantly aspen support the greatest density of breeding chestnut-sided warblers. Northern Hardwood Forest that is dominated by maple–basswood–aspen is also important. Recent attempts by State wildlife agencies to retard vegetational succession by clear-cutting or selectively logging mature deciduous forest are beneficial for this warbler.

Bay-breasted Warbler (*Dendroica castanea*)

Status: Regular migrant.

Migration: Uncommon to rare spring migrant in the Western Upland and Central Plain; fairly common in the Northern Highland. Common fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 8–12 May, reaching the Northern Highland about 15 May. Peak migration occurs 15–25 May and departure by 1 June. Jackson (1943) reported that the collection of a female bay-breasted warbler at Danbury, Douglas County, on 27 May 1919 was the only spring record obtained in northwestern Wisconsin that year. Fall migrants arrive in the Northern Highland in late July, reaching the Western Upland 10–15 August. Peak fall migration occurs 1–20 September. Departure from the Northern Highland occurs 20–25 September and elsewhere by 1 October (latest—19 October 1968, Chisago County).

Habitat: Bay-breasted warblers occupy a wide range of deciduous and coniferous habitats. In the Northern Highland they are most regularly observed in Lowland Coniferous Forest or Black Spruce–Tamarack Bog.

Blackpoll Warbler (*Dendroica striata*)

Status: Regular migrant.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 5-10 May (earliest—30 April 1967; 1 May 1969, Washington County) and the Northern Highland 10-15 May. Peak spring migration occurs 15-25 May and departure is by 30 May (latest—2 June 1970, Washington County). Fall migrants arrive in the Northern Highland 10-15 August and reach the Western Upland 15-20 August. Peak fall migration occurs 30 August to 20 September and departure 25-30 September.

Habitat: Although both deciduous and coniferous forest habitats are regularly used, this warbler is the most common in mature deciduous forest.

Pine Warbler (*Dendroica pinus*)

Status: Regular migrant and nesting species.

Migration: Uncommon to rare migrant throughout the Valley. Jackson (1943) found this warbler not as plentiful as anticipated in 1919. However, they were considered "common" at Danbury, Burnett County, 27-30 May 1919. Spring migrants arrive in the Western Upland 1-5 May and the Northern Highland 5-10 May. This species is most frequently encountered 10-20 May. Departure from nonbreeding areas occurs by 25 May. Fall migration begins in the Northern Highland 10-15 August and the first birds reach the Western Upland 20-30 August. This species is most frequently encountered 1-15 September and they have departed by 1 October.

Nesting Season Distribution: Uncommon breeding species in the Northern Highland, rare and local in the Central Plain. Breeding Bird Survey data (Table 6) also suggest that this species is in the Western Upland during the nesting season. Although breeding season records exist for all areas except Pierce and Washington counties, confirmed nest records exist only for Pine County. Territorial birds were recorded in Chisago County during the summers of 1973-74 and 1976. The only location of regular occurrence in St. Croix County is near Burkhardt (Sec. 3, T. 29 N., R. 19 W.).

Habitat: Characteristic nesting species of remnant white pine forest. Although regularly recorded in Jack Pine Barrens, Breeding Bird Survey data for the Union transect (Burnett County) suggest that low densities occur in that habitat.

Palm Warbler (*Dendroica palmarum*)

Status: Regular migrant, probable nesting species.

Migration: Abundant migrant throughout the Valley, probably second only to the yellow-rumped warbler in overall abundance. Spring migrants arrive in the Western Upland 25 April to 1 May, reaching the Northern Highland 1-5 May. Peak migration occurs 5-15 May and departure by 25 May. A singing male in Chisago County on 4 June 1968 was undoubtedly a very late migrant. Fall migrants arrive in the Northern Highland 20–25 August and the Central Plain 25 August to 5 September. Peak fall migration occurs 10–25 September and birds depart by 10 October (latest—25 October 1968, Chisago County).

Nesting Season Distribution: This species probably nests in Douglas County (S. D. Robbins, personal communication). On 27 June 1966, Robbins heard a singing male palm warbler in a bog in Sec. 35, T. 43 N., R. 12 W. On 26 June 1974 a male was heard in Sec. 23, T. 43 N., R. 12 W. On the same date another male palm warbler was recorded in a large open bog 6.4 km north of Moose Junction (T. 44 N., R. 14 W.).

Habitat: In the Western Upland and Central Plain, palm warblers occupy medium-aged deciduous forest extensively. Alder Thicket and Shrub Carr are also important. In the Northern Highland, extensive use is made of Lowland Coniferous Forest, Black Spruce–Tamarack Bogs, and sedge meadow. Nesting season records are of birds in open Black Spruce–Tamarack Bogs.

Ovenbird (*Seiurus aurocapillus*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland about 1 May and the Northern Highland 5–10 May. Peak spring migration occurs 10–20 May. Departure from nonbreeding areas of the Western Upland occurs by 25 May. Peak fall migration is 1 September (Northern Highland) to 10 September (Western Upland) and departure is by 1 October.

Nesting Season Distribution: Common to locally abundant breeding bird in the Northern Highland and Central Plain. Uncommon and local in the Western Upland. Breeding Bird Survey data (Table 6) indicate that this warbler occurs in greatest numbers in the Northern Highland and Central Plain. Jackson (1943) referred to the ovenbird as the characteristic and often dominant breeding bird in heavier deciduous forest (= mature Northern Hardwood). Goddard (1972) reported the ovenbird was the most abundant breeding warbler in the Lower Kinnickinnic River Valley, Pierce County.

Habitat: Characteristic nesting species of mature Northern Hardwood Forest, where the predominant tree species include sugar maple, basswood, trembling aspen, and white birch. In the Western Upland, breeding ovenbirds are associated with red oak–Hill's oak forest. Remnant stands of mixed red pine and white pine are regularly used in the northern regions.

Northern Waterthrush (*Seiurus noveboracensis*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant in the Western Upland and Central Plain, locally common in the Northern Highland. Spring migrants arrive 1–5 May, reaching the Northern Highland 5–10 May. Peak migration occurs 10–20 May and departure from nonbreeding areas is by 30 May. Fall migrants arrive in the Northern Highland about 5 August, reaching the Western Upland 20–25 August (earliest—12 August 1962, St. Croix County). Peak fall migration occurs 25 August to 10 September and departure by 30 September.

Nesting Season Distribution: Rare and local breeding species, occurring primarily in the Northern Highland. Most observations of nesting season northern waterthrushes have been in habitats along and adjacent to the St. Croix River in Douglas, Burnett, and Pine counties. Breeding Bird Survey data show the low breeding density of this species in the Valley. Goddard (1972) reported a northern waterthrush during the breeding season along the Kinnickinnic River, Pierce County, in June 1971. If correct, that record would extend the probable breeding range of this species at least 160 km south. The lack of proper habitat, plus the population of Louisiana waterthrush along the river, render that record suspect.

Habitat: This species uses a narrow range of wet habitats in the Northern Highland. Primary breeding habitat includes Lowland Coniferous Forest, Alder Thicket, and Northern Sedge Meadow that is becoming invaded with various shrubs including smooth alder and gray dogwood. During migration in the Western Upland and Central Plain, Lowland Deciduous Forest, Northern Hardwood Forest, and Deciduous Clear Cuts are used extensively, as are shorelines of lakes and streams.

Louisiana Waterthrush (*Seiurus motacilla*)

Status: Regular migrant and nesting species.

Migration: Rare spring migrant in the Western Upland and Central Plain. Records in the Central Plain are restricted to areas south of St. Croix Falls and Taylor's Falls. No well-defined pattern of spring migration can be established. Most birds observed appear to be on established breeding territories. Most spring individuals occur 10–30 May (earliest—27 April 1964 [Soulen 1965], 2 May 1948, and 3 May 1966; Washington County). Fall migration is early and diffuse (latest—23 August 1974, Chisago County; 11 September 1972, St. Croix County).

Nesting Season Distribution: Rare and local nesting species of the Western Upland and Central Plain. Confirmed breeding records exist for Chisago (Green and Janssen 1975), Washington, and St. Croix counties. Breeding season birds have also been recorded in Pierce and Polk counties; however, nest records are lacking.

Probably the best-known breeding area in the Valley for Louisiana waterthrush is along Lawrence Creek near Franconia, Chisago County. Longley (1973*b*) described the first known breeding record of this bird at that location, when a nest containing two young cowbirds, one young Louisiana waterthrush, and one addled egg was found near Franconia on 9 June 1973. In June 1968 Longley (1973*b*) recorded six singing males at this same locality. One Louisiana waterthrush was also recorded at that location in 1974–76 and a nest was found in 1975.

Another well-known nesting area is along the lower Willow River near the

Trout Brook Road bridge at Hudson, St. Croix County. At that location, Louisiana waterthrush has been recorded in the breeding season intermittently since 1960. On 3 June 1974 I recorded singing males at four locations along a 300-m reach of this stream. Returning on 5 June 1975, I located two singing males and found one nest containing three eggs; their outcome is unknown.

Elsewhere, records from Washington County include one nest at Stillwater on 10 July 1943 (Chambers 1944) and a nest containing five young on 17 June 1945 (Lupient 1945). Roberts (1938) described the observation of a nest and young along the St. Croix River below Taylor's Falls, Chisago County, on 2–4 July 1927. Goddard (1972) reported this species during June 1971 along the Lower Kinnickinnic River, Pierce County. In the area near the mouth of that river, two to three singing males have been recorded yearly in June 1973–78, but no nest has been found.

Habitat: Rich stands of Lowland Deciduous Forest along fast-moving streams. The St. Croix County nest was located beneath an overhanging root of American elm, less than 1 m from water's edge.

Kentucky Warbler (*Oporornis formosus*)

Status: Casual, two records.

Record: S. D. Robbins observed a male Kentucky warbler near Roberts, St. Croix County, on 28 May 1963 (Faanes and Goddard 1976). This observation represents the most northerly record of this warbler in Wisconsin. Glassel (1977) described the observation of a singing male Kentucky warbler on 17 June 1977 at Afton State Park, Washington County. The bird remained in the area at least until 19 June 1977.

Connecticut Warbler (*Oporornis agilis*)

Status: Regular migrant and nesting species.

Migration: Rare spring and uncommon fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–20 May (earliest—4 May 1974, Pierce County), and reach the Northern Highland about 25 May. During spring they are most frequently observed 25 May to 5 June and depart by 10 June. Fall migrants arrive 15–20 August in the Northern Highland and 20–25 August in the Western Upland. Peak fall migration occurs 5–15 September and they depart by 25 September. Roberts (1938) mentioned the observation of "several" Connecticut warblers in Pine County during the first week of October 1929.

Nesting Season Distribution: Rare and local during the nesting season. Gromme (1941) described the only confirmed breeding of this warbler in the Valley; a nest containing four young on 7 July 1941, near Gordon, Douglas County (T. 43 N., R. 13 W.). Green and Janssen (1975) showed that the nesting range of this warbler in Minnesota reached northern Pine County. Breeding Bird Survey data (Table 6) suggest that a fairly large breeding population exists in southern Douglas County (Sec. 11, 12, 13, 14, T. 43 N.,

R. 12 W.; Robbins 1974*a*). Another population is known to occur in northwestern Burnett County near Grantsburg.

Habitat: Bent (1953) described the breeding habitat of the Connecticut warbler as consisting of tamarack bogs or wet coniferous forest. However, Robbins (1974*a*) reported this warbler in fairly large densities in monotypic stands of jack pine. Further description of this habitat indicates the trees were 4–9 m high and had well-developed lower branches. Trees < 4.6 m tall or those with a scarcity of lower branches were not used by breeding Connecticut warblers. Robbins' observation of nesting in jack pine is further substantiated by recent (1974–78) records from the Union BBS transect, Burnett County. The habitat along this route also consists of large tracts of jack pine, and Connecticut warblers have been found regularly there.

Mourning Warbler (*Oporornis philadelphia*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 May and reach the Northern Highland 15–20 May. Peak spring migration occurs 25 May to 5 June and departure from nonbreeding areas by 10 June. Fall migrants arrive in the Western Upland 20–25 August. Peak fall migration through the Valley occurs 5–15 September and departure by 25 September (latest—29 September 1965, Washington County).

Nesting Season Distribution: Fairly common (locally common) breeding bird in the Northern Highland and the northern half of the Central Plain. Elsewhere, the mourning warbler is uncommon to rare during the nesting season. A nest with young observed in Washington County on 11 and 13 July 1975 (Eckert 1975) represents the southernmost breeding record in the Valley. Breeding Bird Survey data (Table 6) also suggest that the mourning warbler breeding population increases with latitude through the Valley.

Habitat: Characteristic breeding habitat of the mourning warbler includes Northern Hardwood Forest and Deciduous Clear Cuts. Primary nesting habitat of this warbler appears to be areas of dense understory in mature stands of deciduous forest, such as those resulting from openings in the overstory that allow ample sunlight to penetrate. The edge between medium-aged aspen forest and open fields or highway rights-of-way are also important habitats. I have not recorded this warbler in coniferous habitats during the breeding season.

Common Yellowthroat (*Geothlypis trichas*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 1–5 May and the Northern Highland about 10 May. Peak spring migration occurs 10–20 May. Fall migration begins about 15 August. Peak fall migration through the Valley occurs 5–20 September and departure by 5 October (latest—17 October 1955, Polk County).

Nesting Season Distribution: Abundant and well-distributed breeding bird in all regions. Confirmed nest records have been obtained from all counties. Goddard (1972) reported that the common yellowthroat was the second most abundant breeding warbler in the Kinnickinnic River Valley, Pierce County. Breeding Bird Survey data (Table 6) suggest that the common yellowthroat is the most obvious, if not the most abundant, breeding warbler in the Valley. The greatest relative abundance occurs in the Northern Highland and in northern areas of the Central Plain.

Habitat: The common yellowthroat is nearly unlimited in its choice of nesting habitat. Jackson (1943) found this warbler in "damp brushy woodland." In the Western Upland, common yellowthroats are most abundant in small patches of mixed willow and cottonwood associated with streams or rivers. In the Central Plain, extensive use is made of the cattail–bulrush vegetation associated with seasonally and semipermanently flooded wetlands; Shrub Carr and sedge meadow are also important. In the Northern Highland, this warbler uses Alder Thickets, Northern Sedge Meadows, and Forest Bordered Lakes. Tamarack bogs and Lowland Coniferous Forest are also important. Use of upland habitats include dry upland fields and brushy edge areas.

Yellow-breasted Chat (*Icteria virens*)

Status: Casual migrant and summer resident.

Migration: There are two spring records from St. Croix County: 6 May 1964 and 18 May 1962. Both observations were made along Trout Brook Road near Hudson. One fall record (22–29 September 1948) exists for St. Croix Falls, Polk County (Robbins 1949).

Nesting Season Distribution: S. D. Robbins observed singing male yellow-breasted chats near Hudson and Burkhardt, St. Croix County, on 17 June 1961, 21 June 1963, and 30 June 1964. The habitat associated with these birds consisted of various shrubby plants at the border of agricultural fields and (one bird) the edge of a retired hayfield. These habitats are similar to typical breeding habitat within their normal range. Thus, it is likely at that date that these were males defending territories or at least advertising for a mate.

Habitat: This species is most frequently encountered in the Old Field Community and brushy edges of Southern Deciduous Forest.

Hooded Warbler (*Wilsonia citrina*)

Status: Casual, two spring records.

Records: S. D. Robbins observed a singing male hooded warbler at the entrance to Birkmose Park in Hudson, St. Croix County, on 29 May 1963 (Faanes and Goddard 1976). A male hooded warbler was banded and photographed in Washington County on 2 June 1962 (Olyphant 1962).

Wilson's Warbler (*Wilsonia pusilla*)

Status: Regular migrant.

Migration: Fairly common (locally common) migrant throughout the Valley. Spring migrants arrive in the Western Upland about 10 May (earliest—4 May 1966, Washington County) and reach the Northern Highland from 10-15 May. Peak spring migration occurs 15-25 May and departure is by 1 June. Fall migrants arrive in the Northern Highland 10-15 August and the Western Upland about 20 August. Peak fall migration occurs 25 August to 10 September and departure is by 25 September (latest—27 September 1967, Washington County).

Habitat: Wilson's warbler uses a variety of deciduous and coniferous habitats during migration. Although no single habitat is of major importance, this species is most frequently observed in brushy fencerows, Deciduous Clear Cuts, and young to medium-aged Northern Hardwood Forest dominated by trembling aspen and white birch.

Canada Warbler (*Wilsonia canadensis*)

Status: Regular migrant and summer resident.

Migration: Uncommon migrant throughout the Valley. The Canada warbler is among the latest arriving warblers during spring migration. The first birds reach the Western Upland 12-15 May and the Northern Highland 15-20 May. Peak spring migration occurs 20-30 May and departure from nonbreeding areas by 30 May (latest—2 June 1970, Washington County). The first fall migrants arrive in the Western Upland 5-10 August. Peak fall migration occurs 15 August to 5 September and departure by 15 September (latest—29 September 1967, Washington County).

Nesting Season Distribution: Rare and local during the breeding season, apparently restricted to the Northern Highland. Breeding Bird Survey data (Table 6) also suggest restriction to the Northern Highland. The breeding range of this warbler in the Minnesota counties is known to include only northern Pine County (Green and Janssen 1975).

Habitat: Primarily encountered along the edge of Northern Hardwood Forest and in Lowland Coniferous Forest during the nesting season. My observations of this bird's breeding habitat suggests that brushy understory associated with Northern Hardwood Forest is probably most regularly used. Deciduous Clear Cuts in the Northern Highland receive moderate use as does the brushy edge between aspen forest and adjacent open areas.

American Redstart (*Setophaga ruticilla*)

Status: Regular migrant and nesting species.

Migration: Common (locally abundant) migrant throughout the Valley. Spring migrants arrive in the Western Upland 1-5 May and reach the Northern Highland 5-10 May. Peak spring migration occurs 10-25 May.

During 1919, Jackson (1943) reported that American redstarts were "the commonest of the warblers" at St. Croix Falls, Polk County, and he found them "abundant" in timber along the St. Croix River. Fall migration begins 5-10 August in the Northern Highland and 20-25 August elsewhere. Peak fall migration occurs 25 August to 15 September and departure is by 5 October (latest—13 October 1966, Washington County).

Nesting Season Distribution: Common nesting species throughout the Valley. Locally abundant in the Western Upland and Central Plain, in areas associated with the mouths of major streams. Goddard (1972) reported a density of 3.9 pairs per 40 ha in the lower Kinnickinnic River Valley, Pierce County. However, his study area was primarily upland deciduous forest, which is not preferred habitat of breeding American redstarts. Breeding Bird Survey data (Table 6) suggest that highest breeding densities occur in the Central Plain and Northern Highland. Unfortunately, this route of survey does not traverse important American redstart habitat directly adjacent to the St. Croix River and its tributaries in the Western Upland.

Habitat: Characteristic breeding bird of Lowland Deciduous Forest in the Western Upland and Central Plain. Vegetation of these areas includes American elm, box elder, green ash, and basswood. Important upland habitat in the Northern Highland includes medium-aged to mature Northern Hardwood Forest that is dominated by basswood, maple, big-toothed aspen, and white birch. Use of coniferous habitats by nesting American redstarts is very light.

FAMILY PLOCEIDAE: Weaver Finches

House Sparrow (*Passer domesticus*)

Status: Introduced permanent resident.

Distribution: Common to locally abundant resident throughout the Valley. The largest concentrations of house sparrows occur in residential areas and other sites of human habitation, including rural residential developments and farms. This species is less numerous and more localized in heavily forested habitats away from the influence of humans.

Habitat: Closely related to areas of human settlement including houses, office buildings, feedmills, railroad tracks, farmyards, feedlots, and pastures.

FAMILY ICTERIDAE: Meadowlarks, Blackbirds, and Orioles

Bobolink (*Dolichonyx oryzivorus*)

Status: Regular migrant and nesting species.

Migration: Common to locally abundant migrant in Western Upland and Central Plain, uncommon and local in the Northern Highland. Spring migrants arrive 25 April to 1 May, reaching northern areas by 10 May. Peak spring migration occurs 10–20 May. Fall migration begins in late July in the Northern Highland and 10–15 August elsewhere. Peak abundance occurs 20–30 August and departure from the Northern Highland by 20 August and 15 September elsewhere.

Nesting Season Distribution: Common to locally abundant nesting species in Western Upland and Central Plain. Rare to uncommon and local in the Northern Highland. Breeding Bird Survey data (Table 7) indicate that a uniformly large breeding population occurs in the Western Upland and Central Plain. Documented breeding records exist for Pierce, St. Croix, and Polk counties. There are inferred breeding records for the remainder of the region. In Douglas County, Bernard (1967) referred to the bobolink as a "common summer resident." Jackson (1943) found this species to be "distributed . . . where meadow environment suitable for them prevails"; however, he provided no data for the Valley.

Habitat: Characteristic species of grassland communities including retired cropland, alfalfa fields, tame pasture, Managed Grasslands, and remnant prairies. Occasionally found using Northern Sedge Meadow and Shrub Carr; however, these habitats apparently receive higher use during migration.

Eastern Meadowlark (*Sturnella magna*)

Status: Regular migrant and nesting species, casual in winter.

Migration: Fairly common migrant east of the St. Croix River, uncommon west of the river. Spring migrants arrive 5–15 March, reaching peak abundance 1–15 April. Fall migration begins in early September in the Northern Highland and by 10 September elsewhere. Peak abundance occurs 25 September to 15 October and departure by 1 November.

Nesting Season Distribution: Fairly common nesting species throughout the Valley; most numerous in eastern segments of the Western Upland and

Table 7. *Mean number of bobolinks, meadowlarks and blackbirds recorded on western Wisconsin Breeding Bird Survey transects, 1966–78.*

	Western Upland	Central Plain		Northern Highland	
Species	Hudson	Dresser	Loraine	Union	Minong
Bobolink	31.0	30.7	37.0	0.1	0.5
Eastern meadowlark	3.4	10.7	22.7	0.0	0.4
Western meadowlark	133.7	73.7	32.2	0.1	0.2
Yellow-headed blackbird	4.1	3.4	1.2	0.1	0.5
Red-winged blackbird	50.0	184.4	203.2	8.7	36.0
Northern oriole	7.3	16.3	12.2	3.7	8.3
Brewer's blackbird	0.0	0.6	1.7	0.2	2.7
Common grackle	43.8	84.6	61.2	0.4	10.5
Brown-headed cowbird	11.2	36.1	33.5	24.4	37.9

Central Plain. Documented nesting records exist from St. Croix and Pierce counties. The eastern meadowlark probably nests in the remainder of the Valley. Breeding Bird Survey data (Table 7) demonstrate a marked increase in relative abundance moving eastward from the St. Croix River. These population indices range from an average of 3.4 per year on the Hudson BBS (St. Croix County), to 22.7 per year on the Loraine BBS (Polk County).

Winter: Several winter records exist for this species, primarily from Washington County. These records include one on the St. Paul Suburban CBC 30 December 1961 and two on this count 30 December 1972. There are two winter records from Wisconsin: three birds that I netted on 16 January 1975 in Pierce County and one bird near Deronda, Polk County, during the 1947-48 winter (Robbins 1948*b*).

Habitat: Eastern meadowlarks occupy a variety of grassland habitats including domestic hayfields, retired croplands, remnants of oak savannah habitats, overgrazed pasture, Old Field Communities, and drier portions of Shrub Carr wetlands.

Western Meadowlark (*Sturnella neglecta*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common to abundant migrant in the Western Upland and Central Plain, fairly common in the Northern Highland. Spring migrants arrive in the Western Upland 5-10 March and reach the Northern Highland 25 March to 5 April. Peak abundance occurs 25 March to 15 April. Fall migration begins in mid-August in the Northern Highland and by 1 September elsewhere. Peak abundance occurs 20 September to 20 October and departure by 1 November; occasional stragglers remain to 1 December.

Nesting Season Distribution: Common to locally abundant breeding species in all regions. Breeding Bird Survey data (Table 7) demonstrate a marked increase in relative abundance westward through the Valley. Average numbers recorded per route range from <1 in Douglas County (Minong BBS) and 32.2 in Polk County (Loraine BBS) to 133.7 in St. Croix County (Hudson BBS). This trend in breeding population distribution is the reverse of the eastern meadowlark.

Winter: Meadowlarks are fairly regular during winter months in the Western Upland. Many of these records are probably referable to western meadowlark; however, plumages are similar to the eastern meadowlark, which confounds identification.

Habitat: Highest density breeding populations occur in retired croplands and Managed Grasslands where characteristic vegetation includes timothy, brome grass, quack grass, and intermediate wheat grass. Nesting western meadowlarks also use heavily grazed pastures, Hayland, remnant prairie associated with oak savannah, and Old Field Communities. In the Central Plain and Northern Highland, nesting pairs occasionally occupy drier portions of Northern Sedge Meadow.

Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)

Status: Regular migrant and nesting species.

Migration: Fairly common (locally common) migrant in the Western Upland, uncommon and local in the Central Plain, and rare in the Northern Highland. Spring migrants arrive in the Western Upland about 15 April, reaching the Northern Highland by 1 May. Peak spring abundance occurs 1–15 May and nonbreeding birds depart by 20 May. Fall migration begins with dispersal from breeding marshes and the formation of loose flocks in late July. Peak fall abundance occurs 15 August to 1 September and departure by 30 September (latest—9 October 1966, Washington County).

Nesting Season Distribution: Common to locally abundant breeding bird in central St. Croix, Washington, and southern Polk counties. I conducted a census of breeding yellow-headed blackbirds in 1975 and found over 1,000 pairs in central St. Croix County; a 1977 census yielded fewer than 500 pairs. The difference was attributed to persistent drought conditions. Documented breeding records exist for St. Croix, Washington, Polk, and Burnett counties. Breeding Bird Survey data (Table 7) suggest that the largest breeding populations occur in the Western Upland. An isolated breeding population exists at Crex Meadows Wildlife Area, Burnett County. Ellarson (1950) reported two additional colonies in Burnett County in 1948 and 1949 which were still occupied in 1977. Green and Janssen (1975) stated that this species is absent from "much of Pine County."

Habitat: Characteristic nesting species of deep semipermanently and permanently flooded wetlands. Predominant vegetation associated with yellow-headed blackbird nesting habitat includes cattail, river bulrush, hardstem bulrush, and phragmites.

Red-winged Blackbird (*Agelaius phoeniceus*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant throughout the Valley. Spring migrants arrive in late February in the Western Upland, reaching the Northern Highland by 15 March. Peak spring migration occurs 15 March to 10 April. Fall migration begins in mid-July with dispersal from nesting areas and the formation of loose flocks. Numbers gradually build through August reaching peak abundance 10–25 September. During this period, roost flocks ranging from 25,000 to 50,000 individuals can be observed. Most fall migrants have departed by 1 November; however, stragglers remain into early December.

Nesting Season Distribution: Abundant nesting species in the Western Upland and Central Plain, common in the Northern Highland. Breeding Bird Survey data (Table 7) suggest that a very large breeding population exists in the open agricultural areas of the Western Upland and Central Plain. This breeding population diminishes in abundance in the more forested Northern Highland.

Winter: Regular winter resident in the Western Upland, casual elsewhere. Wintering red-winged blackbirds are usually associated with Lowland Deciduous Forest, Shrub Carr, Alder Thicket, natural basin wetlands, farmsteads, and feedlots.

Habitat: Red-winged blackbirds use a variety of wetland and upland sites for nesting. Wetlands include sedge meadows, seasonally, semipermanently, and permanently flooded wetlands dominated by cattail, river bulrush, hardstem bulrush, softstem bulrush, and phragmites. Alder Thicket, Shrub Carr, northern Forest Bordered Wetlands, and Black Spruce–Tamarack Bogs are also important. Upland nesting sites include agricultural fields, Old Field Community, Hayland, Managed Grasslands, and to a lesser extent Northern Hardwood Forest, Southern Deciduous Forest, and Lowland Deciduous Forest. This species is among the most widespread and adaptable breeding birds in the Valley.

Orchard Oriole (*Icterus spurius*)

Status: Casual migrant and nesting species.

Migration: Rare migrant in Pierce, St. Croix, and Washington counties; accidental elsewhere. Migrants arrive 15–20 May, remaining in this region until mid-August. There are two spring records for Polk County: 20 May 1949 and 20 May 1976.

Nesting Season Distribution: Several nesting season records exist in the Western Upland; however, only one confirmed nesting record exists. A nest with eggs was found in Washington County on 15 July 1953 (Herz 1954). S. Sprunt found a singing male near Gordon, Douglas County, on 6 July 1956 (Lound and Lound 1956*b*). Recently, nesting season adults have been regularly observed along the lower Willow River in St. Croix County. Although nest records have not been obtained here, strong evidence of nesting exists.

Habitat: Breeding season orchard orioles are typically associated with open areas in mature Lowland Deciduous Forest.

Northern Oriole (*Icterus galbula*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley, locally abundant adjacent to the St. Croix River in St. Croix, Pierce, and Washington counties. Spring migrants arrive in the Western Upland 1–5 May and peak populations occur 15–20 May. Spring migrants arrive in the Northern Highland by 10 May (earliest—26 April 1957, Burnett County; Lound and Lound 1957*c*), reaching peak populations 20–25 May. Fall migration begins in late July. Peak movement in the Northern Highland occurs 5–20 August and departure is by 10 September. Peak fall migration in the Western Upland occurs 15–30 August and departure is by 15 September (latest—1 December 1971, Washington County).

Nesting Season Distribution: Common nesting species in the Western

Upland and Central Plain, uncommon and local in the Northern Highland. Breeding Bird Survey data (Table 7) suggest that the region of greatest abundance is the Central Plain. Unfortunately, the Hudson BBS route does not traverse large expanses of northern oriole habitat as this species is a common breeding bird in that area. A recent increase in breeding populations is suggested by Jackson's (1943) statement that this species was "nowhere common in the region except at St. Croix Falls," (Polk County). Goddard (1972) reported a density of 20.7 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: The northern oriole is primarily a species of mature deciduous forest. Also fairly common in ornamental plantings in residential areas. The largest breeding populations occur in mature Northern Hardwood Forest and Lowland Deciduous Forest.

Rusty Blackbird (*Euphagus carolinus*)

Status: Regular migrant and occasional early winter resident.

Migration: Common spring and abundant fall migrant throughout the Valley. Spring migrants arrive in the Western Upland about 10 March and reach the Northern Highland by 25 March. Peak spring populations occur 1–20 April and departure is by 5 May. Fall migrants arrive about 15 September, reaching peak populations 10–25 October. Most have departed from the Northern Highland by 10 November and elsewhere by 1 December.

Winter: Early winter records of this species consist primarily of small flocks associated with lowland forest habitats. Christmas Bird Count data suggest that early winter occurrences are restricted largely to areas adjacent to the lower St. Croix River. However, one record of an individual on the Solon Springs CBC was probably of a late migrant. During January and February, single birds will occasionally frequent feeding stations, including one at a Polk County feeder through 17 February 1959 (Winkler 1959).

Habitat: The rusty blackbird is primarily a species of wetland habitats. Fall concentrations of these birds are typically observed in large Alder Thickets, Shrub Carr, or northern bog habitats. Edges of prairie wetlands are also heavily used, primarily in the Western Upland.

Brewer's Blackbird (*Euphagus cyanocephalus*)

Status: Regular migrant and nesting species.

Migration: Fairly common spring and uncommon fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 March, reaching the Northern Highland by 1 April. Peak migration occurs 10–30 April and departure from nonbreeding areas by 10 May. Fall migrants arrive in the Western Upland 10–15 August. Peak fall populations occur 25 August to 15 September and departure is by 10 October.

Nesting Season Distribution: Fairly common to locally uncommon nesting species in the Central Plain and Northern Highland. Roberts (1932) described the eastward extension of this species' breeding range from the Red River Valley to east-central Minnesota in the early 1900's. Additional evidence of recent expansion into this region is provided by Jackson (1943) who failed to record this bird in northwestern Wisconsin in 1919.

Winter: Several CBC records of Brewer's blackbird exist for the Suburban St. Paul count. These records include: 4 on 29 December 1962, 4 on 26 December 1964, and 11 on 30 December 1972.

Habitat: Brewer's blackbirds primarily use fencerows, railroad rights-of-way and Old Field habitats. Occasional breeding pairs are encountered in Northern Sedge Meadow, open bog habitats, and in highway rights-of-way.

Common Grackle (*Quiscalus quiscula*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant in the Western Upland and Central Plain, fairly common (locally common) in the Northern Highland. Spring migrants arrive in the Western Upland 20–25 February, reaching the Northern Highland by 30 March. Peak populations occur 20 March to 15 April. Fall migration begins in mid-July with dispersal from breeding areas. Large mixed flocks of common grackles and red-winged blackbirds form in early August, supplemented with Brewer's blackbirds in late August and rusty blackbirds in late September. Peak fall populations occur 10 September to 10 October. Departure from the Northern Highland occurs by 15 October and most birds have departed from the Western Upland by 5 November but stragglers remain to 30 November.

Nesting Season Distribution: Common to locally abundant nesting species in the Western Upland and Central Plain, uncommon to locally common in the Northern Highland. This is one of the most rapidly increasing nesting species in the Valley. Breeding Bird Survey data (Table 7) show a gradual decrease in relative abundance northward from the heavily farmed regions of the Western Upland. In 1919, Jackson (1943) reported that common grackles were "never particularly plentiful, except when they gathered in flocks." The current abundance of this species and the expansion of its breeding range has been fairly recent and may be associated with an expanding human population or changes in agricultural practices.

Winter: Common grackles occasionally overwinter each year in the Western Upland. Individual birds elsewhere may be wintering or late migrants.

Habitat: Common grackles are fairly opportunistic in their selection of nesting habitats and have been recorded in nearly every habitat type. Highest breeding densities are usually associated with Pine Plantations, deciduous woodlots, or ornamental conifer plantings. The increased planting of coniferous trees has enhanced common grackle nesting populations and may be a factor in their expanding and increasing populations.

Brown-headed Cowbird (*Molothrus ater*)

Status: Regular migrant and nesting species, casual early winter resident.

Migration: Abundant spring and uncommon fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 15-20 March and reach the Northern Highland by 10 April. Peak spring populations occur 10-25 April. Fall migration begins with flock formation in late June. A gradual movement away from breeding areas occurs throughout the fall; consequently, no peak population dates can be given. Most migrants have departed by 15 September and stragglers remain through October.

Nesting Season Distribution: Common to locally abundant nesting species throughout the Valley. Breeding Bird Survey data (Table 7) show a large and well-distributed breeding population. Goddard (1972) reported a density of 24.2 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Winter: Several early winter records exist from CBC's in Washington, St. Croix, and Douglas counties. These records include: 1 January 1970 (St. Croix); 1 January 1975, and 3 January 1976 (Washington); and 18 December 1974 (Douglas).

Habitat: Brown-headed cowbirds use virtually all habitats in this region. Largest breeding populations occur in woodland edge situations.

FAMILY THRAUPIDAE: Tanagers

Scarlet Tanager (*Piranga olivacea*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 1-5 May, reaching the Northern Highland 5-10 May. Peak spring migration through the Valley occurs 10-25 May. Fall migration begins in mid-August. Peak fall migration occurs 25 August to 15 September and departure by 1 October.

Nesting Season Distribution: Fairly common nesting species throughout the Valley. This species is more widespread and probably occurs in greater densities in the Central Plain and Northern Highland. Bernard (1967) considered the scarlet tanager a common summer resident in Douglas County. Jackson (1943) reported this species as common at St. Croix Falls, Polk County, and mentions the observation of mated pairs at that location. Goddard (1972) reported a density of 4.5 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: Characteristic nesting species of deciduous forest communities. Habitat use by nesting scarlet tanagers varies with geomorphic province. In the Western Upland, this species is most abundant in mature Lowland Deciduous Forest and Southern Deciduous Forest. In the Central Plain and Northern Highland, scarlet tanagers are most abundant in mature Northern Hardwood Forest and in early successional stage aspen forest. Breeding pairs in Jack Pine Barren habitat are normally found in the "scrub" oak savannahs interspersed with jack pine.

Summer Tanager (*Piranga rubra*)

Status: Casual, two records.

Records: One male was observed in Polk County on 18 May 1956 (Lound and Lound 1956*a*). Another male was observed at Grantsburg, Burnett County, on 29 September 1967 (Caldwell 1968).

FAMILY FRINGILLIDAE: Grosbeaks, Finches, Sparrows, and Buntings

Cardinal (*Cardinalis cardinalis*)

Status: Regular permanent resident.

Distribution: Fairly common (locally common) resident of the Western Upland. Uncommon to rare in the Central Plain, and rare and local in the Northern Highland. Movement of the cardinal into this region has been very recent. In 1919 Jackson (1943) failed to report this bird in northwestern Wisconsin. Young et al. (1941) reported that the first records for Burnett and Pierce counties were in 1920. Roberts (1932) reported several mid-1920 records for the Washington County region. By the 1960's Bernard (1967) considered this bird a rare visitor in Douglas County and mentioned records from Solon Springs. M. Link (personal communication) reported that cardinals were regular at Pine City, Pine County, in 1974.

Breeding season records of the cardinal provide excellent documentation of their decreasing population, which is moving northward through the Valley. Breeding Bird Survey data (Table 8) suggest an abrupt decrease in breeding density from a mean of 1.5 per route in the Western Upland to <0.1 per route in the Northern Highland. Goddard (1972) found the mean density of breeding cardinals in the Kinnickinnic River Valley was 16 pairs per 40 ha.

Winter: Common winter resident in the Western Upland. As shown for the breeding season, the abundance of this bird decreases rapidly as it moves northward. On five CBC's in the Valley, the mean number of cardinals recorded per party hour ranged from 3.1 on the Afton CBC to 0 at Solon Springs (Table 4).

Habitat: Primarily a species of deciduous forest edge during the breeding season. Use of Lowland Deciduous Forest and Southern Deciduous Forest is usually restricted to openings and brushy edges. Highway rights-of-way and windbreaks planted around farmsteads are important, as are shrubbery and ornamental plantings in residential areas.

Rose-breasted Grosbeak (*Pheucticus ludovicianus*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive 1–5 May (earliest—30 April 1978, St. Croix County), reaching peak abundance 10–20 May. Fall migration begins in the Northern Highland

15–25 August. Peak fall migration through the Valley occurs 5–20 September. Departure from the Northern Highland occurs 20–25 September and elsewhere by 5 October (latest—26 October 1965, Washington County).

Nesting Season Distribution: Fairly common (locally common) nesting species in the Western Upland. Population densities apparently increase northward through the Valley. Goddard (1972) reported a density of 31.2 pairs per 40 ha along the Kinnickinnic River Valley in Pierce County; the rose-breasted grosbeak was the fifth most abundant breeding bird in that valley. Breeding Bird Survey data (Table 8) suggest that rose-breasted grosbeaks occur in greatest abundance in the Northern Highland.

Habitat: The rose-breasted grosbeak is a characteristic breeding species of mature deciduous forest and forest edge. In the Western Upland, this grosbeak uses Southern Deciduous Forest dominated by mixed stands of white, red, black, and bur oaks. Also important is mature Lowland Deciduous Forest characterized by cottonwood, green ash, and American elm along the major river systems. In the Central Plain and Northern Highland, primary use is made of mature Northern Hardwood Forest dominated by sugar maple, basswood, trembling aspen, and white birch. Residential Habitats, primarily ornamental shade trees, are also used for nesting.

Table 8. *Mean number of grosbeaks, finches, towhees, and sparrows recorded on western Wisconsin Breeding Bird Survey transects, 1966–78.*

	Western Upland	Central Plain		Northern Highland	
Species	Hudson	Dresser	Loraine	Union	Minong
Cardinal	1.5	0.6	0.0	<0.1	<0.1
Rose-breasted grosbeak	6.0	12.2	18.1	15.0	19.6
Indigo bunting	7.4	8.7	23.3	18.5	18.6
Dickcissel	12.1	6.4	5.4	0.0	0.0
American goldfinch	4.7	9.1	20.6	6.0	5.9
Purple finch	0.0	0.0	0.0	1.0	3.3
Pine siskin	0.0	0.0	<0.1	<0.1	0.2
Rufous-sided towhee	0.2	0.2	0.6	21.7	15.8
Savannah sparrow	17.3	14.1	26.3	0.0	0.3
Grasshopper sparrow	9.6	5.7	6.7	0.7	0.0
Henslow's sparrow	1.2	1.1	0.5	0.0	0.0
Vesper sparrow	18.9	15.3	13.7	6.5	8.6
Dark-eyed junco	0.0	0.0	0.0	0.0	0.6
Chipping sparrow	1.6	6.3	10.9	21.2	24.2
Clay-colored sparrow	4.4	3.0	2.7	7.2	14.9
Field sparrow	7.0	3.2	2.2	10.2	1.9
White-throated sparrow	0.0	0.0	<0.1	0.0	3.5
Lincoln's sparrow	0.0	0.0	0.0	0.0	<0.1
Swamp sparrow	0.0	0.2	0.9	0.2	1.1
Song sparrow	12.9	24.4	32.6	3.5	24.0

Black-headed Grosbeak (*Pheucticus melanocephalus*)

Status: Casual spring migrant.

Records: This western grosbeak has been recorded in the Valley on four occasions. The first record was a male on 27 May 1970 in Washington County (Huber 1974*a*). A female was observed in Washington County 11 May to 1 June 1974, and a male was noted in the same location on 13 May 1974 (Savaloja 1974). I observed a singing male in Glen Park at River Falls, Pierce County, on 25 May 1979 (Eckert 1979).

Indigo Bunting (*Passerina cyanea*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland and Central Plain, uncommon (locally common) in the Northern Highland. Spring migrants arrive in the Western Upland 1–5 May (earliest—26 April 1976, Pierce County) and reach the Northern Highland 5–10 May. Peak spring migration through the Valley occurs 15–30 May. Fall migration begins about 10–15 August. Peak fall migration occurs 1–15 September and departure 20 September to 5 October.

Nesting Season Distribution: Common and well-distributed nesting species in the Western Upland and Central Plain. Fairly common in the Northern Highland, except in regions of extensive coniferous forest. Jackson (1943) considered the indigo bunting an uncommon nesting bird in the Northern Highland in 1919. In the Western Upland, Goddard (1972) found the indigo bunting was the 12th most numerous breeding bird ($\bar{X} = 21.8$ pairs per 40 ha) along the Kinnickinnic River Valley, Pierce County. Breeding Bird Survey data (Table 8) suggest that lowest populations occur in the heavily farmed regions of the Central Plain but increase northward into the Northern Highland.

Habitat: The indigo bunting is a characteristic breeding bird of shrubby "edge" habitat types. In the Central Plain and Northern Highland, Deciduous Clear Cuts under 10 years old receive heavy use by nesting indigo buntings. Important vegetation associated with their breeding habitat includes trembling aspen, box elder, basswood, choke cherry, hazelnut, and prickly ash.

Dickcissel (*Spiza americana*)

Status: Regular migrant and nesting species.

Migration: Common migrant in the Western Upland and Central Plain, rare and local in the Northern Highland. Populations of this bird experience tremendous variations between years and they appear to be cyclic. In adjacent years, dickcissels can vary from among the most numerous migrants in grassland habitats to virtually absent. Spring migrants arrive in the Western Upland and Central Plain 20–30 May and are widespread

1–10 June. During most years, this bird is most numerous during the first 10 days of June. Singing ceases about 1 August and birds become difficult to find after that date. There is no discernible peak in fall migration, and most have departed by 25 August (latest—16 September 1974, Polk County).

Nesting Season Distribution: Fairly common although highly irregular nesting species in the Western Upland and Central Plain. There are no known nest records for Douglas or Pine counties, although Green and Janssen (1975) stated that the breeding range in Minnesota "usually extended only to southern Pine County." Jackson (1943) did not record this species in northwestern Wisconsin during 1919.

During 1975, the dickcissel was virtually absent from St. Croix and Washington counties during the nesting season. In 1976, I recorded a density of 20.4 pairs per 40 ha on Managed Grassland tracts in St. Croix and Polk counties. Breeding Bird Survey data (Table 8) provide another indication of the rapid decrease in abundance moving northward from the Western Upland to Northern Highland.

Habitat: Characteristic breeding bird of retired agricultural fields that have become overgrown with a rank growth of vegetation. Also an important breeding bird of alfalfa fields and of Managed Grasslands that are maintained by various State and Federal wildlife agencies for duck nesting cover.

Evening Grosbeak (*Hesperiphona vespertina*)

Status: Regular migrant and winter resident, casual summer visitor, and possible nesting species.

Migration: Common yet erratic fall and spring migrant in the Western Upland and Central Plain. Usually a common to abundant migrant in the Northern Highland. Migration periods appear to depend upon the abundance of a food source in the northern breeding areas. The first fall migrants usually arrive in the Northern Highland 1–15 October and reach the Western Upland about 15 November, except during invasion years, when they have been recorded in mid-October (15 October 1959, Polk County). Peak fall migration varies with the year, however, usually occurring 15 November to 15 December. Peak spring migration usually occurs during March. During non-invasion years, peak spring migration occurs 25 March to 5 May. The largest late flock on record (600) was observed at Webster (Burnett County) on 25 April 1950. Departure also apparently varies with the year. There are several Polk County departure records that range from 4 May (1954) to 17 May (1952). Latest dates from nonsummering areas include 28 May 1962, Polk County and 30 May 1972, Burnett County.

Nesting Season Distribution: Casual summer resident in the Northern Highland. There are no confirmed nest records for the Valley, although a few pairs may remain to nest after invasion years. Evening grosbeaks were recorded during the 1972 summer in Pine County (Green and Baumhoffer 1972). S. D. Robbins recorded evening grosbeaks along the route of the Minong BBS during mid-June from 1965 to 1977. During June 1974 I observed three male evening grosbeaks in Sec. 14, T. 43 N., R. 15 W., Douglas County, but no evidence of nesting.

Winter: Usually a common to locally abundant winter resident in the Northern Highland. Uncommon to rare (except during invasion years) winter resident in the Central Plain and Western Upland. The highest mean numbers of evening grosbeaks per party hour on CBC are 8.3 at Grantsburg and 3.3 at Solon Springs (Table 4), both in the Northern Highland. The highest count of individuals on CBC's was 739 recorded on the 1974 Grantsburg Count. Considerable variation also exists in yearly totals, which is indicative of the cyclic influxes of this species.

Habitat: Migrant evening grosbeaks use both deciduous and coniferous habitats. Box elder and maple trees that retain their fruits are preferred during migration. Most winter records are obtained from the vicinity of feeding stations, both in rural and urban areas. My records of this bird during the breeding season were obtained from an extensive stand of black spruce adjacent to a stream. This vegetation type appears to be preferred in the northern breeding areas.

Purple Finch (*Carpodacus purpureus*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common migrant in the Western Upland and Central Plain, occasionally abundant in the Northern Highland. Fall migration begins in the Northern Highland about 25 August and the first birds arrive in the Western Upland 15–25 September. Peak fall migration occurs 1 October to 15 November and departure from nonwintering areas by 1 December (latest—18 December 1979, Douglas County). Spring migrants arrive in the Northern Highland about 15 March. Peak spring migration occurs 25 March to 15 April and departure by 1 May (latest—10 May 1970 and 17 May 1966, Washington County).

Nesting Season Distribution: Fairly common nesting species in the Northern Highland. Confirmed nest records exist for Burnett, Polk, and Douglas counties. Green and Janssen (1975) cited an inferred breeding record for Pine County. Breeding Bird Survey data (Table 8) suggest that nesting is restricted to the Northern Highland. The most southerly nest record that I have obtained was a female incubating four eggs on 26 May 1974 near Clam Falls, Polk County (Sec. 11, T. 35 N., R. 15 W.). Jackson (1943) observed a mated pair at St. Croix Falls, Polk County, on 25 May 1919.

Winter: Common (locally abundant) winter resident in the Western Upland. Becomes progressively more scarce in the Central Plain and is virtually absent from the Northern Highland. Christmas Bird Count data (Table 4) demonstrate sharp declines in winter abundance moving northward from the lower St. Croix River. On 1 January 1978, 294 were recorded on the Afton CBC. On 16 February 1979, I banded 105 at a feeding station in Hudson, St. Croix County.

Habitat: During the nesting season, the purple finch is a characteristic species of cool, moist, Lowland Coniferous Forest. Principal vegetation associated with breeding habitat includes black spruce, tamarack, yellow birch, and black ash. All purple finch nests that I have observed were associated with this vegetation type. During migration, purple finches were also found in deciduous habitats, primarily those having heavily seeded box elder. Wintering birds are usually found in black spruce habitat or near feeding stations in residential areas.

Pine Grosbeak (*Pinicola enucleator*)

Status: Regular migrant and winter resident.

Migration: Uncommon fall migrant (occasionally common) in the Northern Highland, rare and irregular fall migrant (occasionally fairly common) in the Central Plain and Western Upland. Less common in all regions during spring migration, except after invasions. On 23 November 1946 pine grosbeaks were already considered "numerous" at Grantsburg, Burnett County. Fall migrants arrive in the Northern Highland 25 October to 15 November. Peak fall migration occurs 15 November to 15 December. Spring migration begins with a gradual northward exodus in late February. Peak spring migration occurs 1–15 March and departure by 1 April (latest—8 May 1974, Polk County).

Winter: Irregular winter resident except for the Northern Highland where wintering pine grosbeaks are observed each year. Winter populations of this bird are considered cyclic. The largest number recorded in the Valley was 436 on the Solon Springs CBC 17 December 1970. Christmas Bird Count data (Table 4) provide supportive evidence of their relative abundance in the various regions of the Valley.

Habitat: Generally restricted to extensive stands of Lowland Coniferous Forest and Jack Pine Barrens. During invasion years, pine grosbeaks use Upland Deciduous Forest, especially if box elder and maple or sumac trees are heavily laden with seeds.

Gray-crowned Rosy Finch (*Leucosticte tephrocotis*)

Status: Accidental, one record.

Record: Ludwig (1974) described the observation of a single gray-crowned rosy finch in Pine County 27 March to 6 April 1974. This was the third record of that species in Minnesota.

Hoary Redpoll (*Carduelis hornemanni*)

Status: Irregular migrant and winter resident.

Migration: During invasion years, a rare migrant in the Northern Highland and Central Plain, casual in the Western Upland. There are too few spring records to establish patterns. Fall migrants usually arrive with the first large flocks of common redpolls in late November (earliest—3 November

1968, Burnett County; 21 November 1950, Polk County). During spring migration, hoary redpolls are observed with common redpoll flocks. Most observations occur in February. Late dates include 4 April 1966, St. Croix County; 6 April 1969, Chisago County; and 12 April 1974, Washington County.

Winter: Rare and irregular winter resident throughout the Valley. Most winter records consist of observations during the CBC periods, usually 15 December to 2 January. The largest number observed (six) was recorded on the Suburban St. Paul CBC 29 December 1973. Considerable debate has been generated concerning the taxonomic status of this bird and the ability of observers to make accurate identification. The most reliable and undoubtedly correct observations are of banded birds. One individual was banded in Chisago County on 1 March 1970. During the winter finch invasion of 1977–78, I banded two hoary redpolls at a feeding station in Hudson, St. Croix County, on 15 February 1978 and 8 March 1978. The latter bird was photographed extensively and copies were deposited with the Wisconsin Society for Ornithology.

Habitat: Regularly observed with flocks of common redpoll in weedy fields and highway rights-of-way.

Common Redpoll (*Carduelis flammea*)

Status: Regular migrant and winter resident.

Migration: Abundant migrant throughout the Valley during periodic invasion years, uncommon to rare migrant during other years. Fall migrants arrive 25 October to 10 November (earliest—12 October 1974, Burnett County). Peak fall migration occurs 15 November to 15 December. Peak spring migration occurs 1–25 March; birds depart from the Central Plain 1–10 April and the Northern Highland by 30 April (latest—30 May 1972, Burnett County).

Winter: Usually an uncommon winter resident except during invasion years when this species becomes one of the most abundant wintering birds. Christmas Bird Count data (Table 4) suggest that the wintering population is fairly well distributed throughout the Valley. The extremely high mean number of common redpolls per party hour on the Solon Springs CBC is skewed upward by a large count during 1977.

The normal 2-year invasion cycle of this bird is shown by comparing the mean number of redpolls per party hour on CBC's throughout the Valley (Fig. 6). Beginning with the 1970 count year, the winter common redpoll population fits a perfect alternate year invasion schedule. Results from the 1977–78 CBC season are considerably higher than other years because the movement of birds that year was one of the largest recorded. The two largest counts on record in the Valley are from the Solon Springs CBC (2,222) and Suburban St. Paul CBC (4,615). The 4,615 is the largest number ever recorded in North America (Monroe 1978).

Habitat: Agricultural fields, retired cropland that has become heavily over-

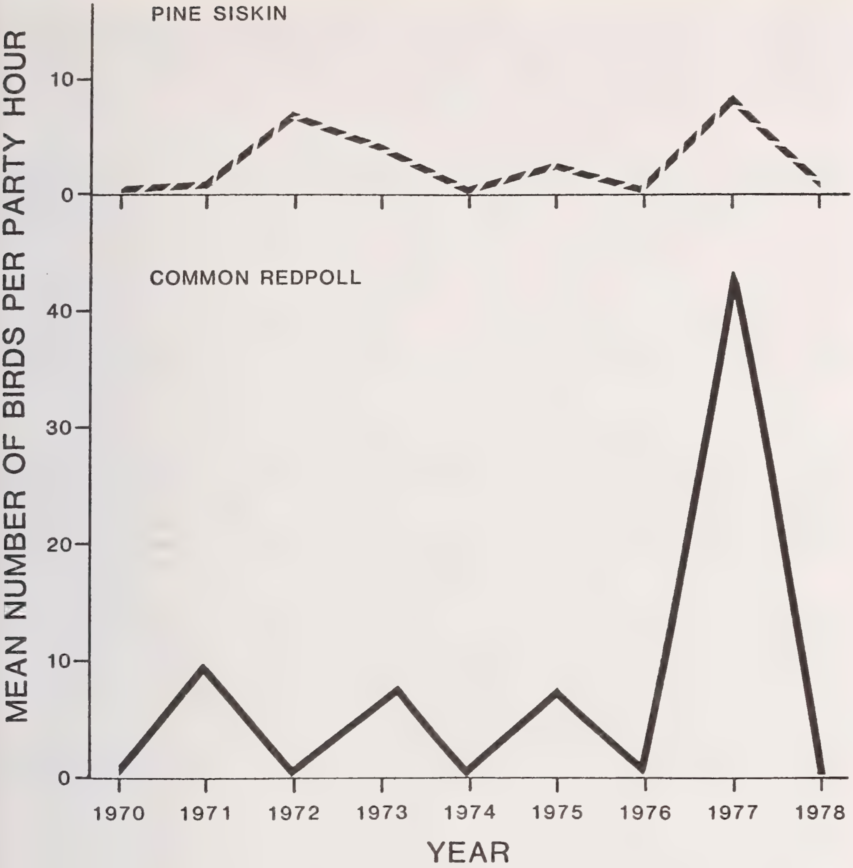

Fig. 6. Patterns of winter abundance of common redpolls and pine siskins in the St. Croix River Valley (data from Christmas Bird Counts).

grown with various weeds, highway rights-of-way, and mixed deciduous–coniferous forest in northern regions.

Pine Siskin (*Carduelis pinus*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Fairly common (occasionally abundant) migrant throughout the Valley. Fall migrants arrive in the Central Plain and Western Upland 15– 25 September. Peak fall migration occurs 10–30 October and departure by 15 November. The number of fall migrants is highly dependent on the intensity of the migration during a given year. Typical of other winter finches, peak movements usually occur during invasion years. Migrants have usually departed the Northern Highland by 1 January, except during years of very high populations when large numbers winter throughout the Valley.

Spring migration begins in late March with a gradual exodus from the southern wintering areas. Spring migration is usually more diffuse than fall and the period of peak movement occurs 10 April to 15 May. Departure from the southern areas occurs 20–30 May.

Nesting Season Distribution: Uncommon nesting species in the Northern Highland. Jackson (1943) reported that pine siskins were "not uncommon" at Solon Springs (Douglas County) from 26 July to 6 August 1919. He does not provide any evidence of nests or young. Larson (1970) reported pine siskins at Taylor's Falls, Chisago County, through the summer of 1969 and until 10 August 1970. No nests or young were reported. On 11 May 1978, I banded a female pine siskin at Hudson, St. Croix County, that possessed a well-defined brood patch. Although no nests or young were observed, pine siskins remained in the area throughout the summer of 1978 and probably nested.

Winter: Fairly common resident in the Western Upland and Central Plain. Uncommon to rare during midwinter in the Northern Highland except during invasion years. Christmas Bird Count data (Table 4) suggest a rapid decline in relative abundance of this species moving northward from the lower St. Croix River Valley. Although not as predictably cyclic as the common redpoll, the pine siskin follows a pattern of abundance 1 year, followed by low numbers for 2–3 years afterward (Fig. 6). Highest daily counts of individuals include 856 on 1 January 1974 (Afton CBC) and 793 on 2 January 1978 (Suburban St. Paul CBC). On 10 February 1961 S. D. Robbins observed over 3,000 pine siskins at Clam Lake, Burnett County.

Habitat: Restricted primarily to coniferous forest during the nesting season. Wintering birds use a variety of coniferous and deciduous habitats. This species makes extensive use of feeding stations in residential areas.

American Goldfinch (*Carduelis tristis*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–30 March, reaching peak abundance 15–30 April. Migrants arrive in the Northern Highland 10–15 April, reaching peak numbers about 1 May. Fall migration begins in mid-August and peak populations occur 15 September to 15 October. Departure from the northern areas occurs by 15 November.

Nesting Season Distribution: Fairly common and well-distributed nesting species throughout the Valley. Jackson (1943) considered the American goldfinch one of the most generally distributed nesting species in northwestern Wisconsin. Breeding Bird Survey data (Table 8) support Jackson's statement. This bird was the fourth most abundant breeding species (33.2 pairs per 40 ha) in the Kinnickinnic River Valley, Pierce County (Goddard 1972).

Winter: Fairly common to locally common winter resident in the Western Upland and Central Plain. Rare and irregular winter resident of the Northern Highland, particularly after mid-January. Christmas Bird Count data (Table 4) suggest a gradual decrease in relative abundance progressing northward. Highest daily counts include 559 on 30 December 1978 (Suburban St. Paul CBC) and 545 on 1 January 1975 (Afton CBC).

Habitat: Typically a nesting species of edge situations including stream banks, brushy edges of woods, highway rights-of-way, and ornamental shrubbery in urban areas.

Red Crossbill (*Loxia curvirostra*)

Status: Regular migrant and winter resident, irregular summer resident, and nesting species.

Migration: Irregular migrant throughout the Valley. During periods of peak occurrence, red crossbills are uncommon except in the Northern Highland where they become locally common. Because of their erratic movements, it is difficult to determine their migration periods, particularly in the Northern Highland. The normal period of occurrence in the Western Upland and Central Plain is 1 October to 1 April; stragglers remain until mid-May.

Nesting Season Distribution: Rare and irregular during the nesting season, primarily in the Northern Highland. Jackson (1943) mentioned the observation of a "flock" at Solon Springs, Douglas County, on 8 August 1919. Jackson (1970) provided the only confirmed nesting record for the Valley when he observed several adults feeding young at Stillwater, Washington County, during May 1970. Larson (1970) found red crossbills near Taylor's Falls, Chisago County, until 5 June 1970 but no evidence of nesting.

Winter: Uncommon and irregular winter resident, usually observed in the Northern Highland. Although this species is dependent on the pinecone crop, population irruptions of red crossbill are not predictable.

Habitat: Breeding season records are typically associated with Lowland Coniferous Forest or Northern Hardwood Forest intermixed with coniferous trees.

White-winged Crossbill (*Loxia leucoptera*)

Status: Regular migrant and winter resident, erratic summer resident.

Migration: Uncommon to rare migrant; most observations are confined to the Northern Highland. Similar in distribution to the red crossbill in occurrence and distribution. During years of peak influxes, white-winged crossbills are locally common to abundant, primarily in the Northern Highland and Central Plain. The normal period of occurrence ranges from 15 October to 15 March.

Nesting Season Distribution: There are no confirmed nest records of this crossbill in the Valley. S. D. Robbins recorded single birds along the route of the Minong BBS, Douglas County, on 11 June 1969 and 21 June 1977. Robbins observed two white-winged crossbills along the route of the Union BBS, Burnett County, on 22 June 1977.

Winter: Uncommon to locally common winter resident in the Northern Highland. Rare to uncommon winter resident elsewhere. During the winter of 1977–78, the movement of this bird into the Valley was among the largest on record. Exceptionally large flocks (200 individuals) were noted, primarily north of St. Croix Falls. These large numbers remained through mid-December. After that time, the number of individuals decreased considerably.

Habitat: This species primarily uses extensive stands of Lowland Coniferous Forest where white spruce is the predominant tree species. Also occasionally observed in mixed coniferous–deciduous forest and Jack Pine Barren.

Green-tailed Towhee (*Pipilo chlorura*)

Status: Accidental, one record.

Record: Garber (1965) reported the observation of one bird at Prescott, Pierce County, on 10 May 1964.

Rufous-sided Towhee (*Pipilo erythrophthalmus*)

Status: Regular migrant and nesting species.

Migration: Uncommon migrant throughout the Valley, common in the Northern Highland. Spring migrants arrive in the Western Upland 25–30 April and the Northern Highland 1–5 May. Peak migration occurs 5–15 May. Peak fall migration occurs 10–25 September and departure by 15 October (latest—8 December 1971, Washington County).

Nesting Season Distribution: Uncommon nesting species throughout the Valley. Jackson (1943) reported that rufous-sided towhees were common at Solon Springs, Douglas County, 28 July to 6 August 1919. Goddard (1972) reported a density of 19.3 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County. Breeding Bird Survey data (Table 8) suggest that the rufous-sided towhee occurs in relatively low numbers in the Western Upland and Central Plain and is common in the Northern Highland.

Habitat: Primarily a species of edge situations. Typical breeding habitat includes semi-open stands of Northern Hardwood Forest (Western Upland). Typical vegetation of these habitats includes second-growth bur oak, trembling aspen, sugar maple, green ash, and basswood. In the Northern Highland, this species becomes particularly numerous in mixed stands of jack pine and oak.

Savannah Sparrow (*Passerculus sandwichensis*)

Status: Regular migrant and nesting species.

Migration: Common spring and fall migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 April and the Northern Highland about 20 April (earliest—30 March 1967, Burnett County). Peak spring migration through the Valley occurs 20 April to 10 May. Peak fall migration occurs 15–30 September and departure by 15 October (latest—25 October 1967, St. Croix County).

Nesting Season Distribution: Fairly common nesting species in the Western Upland and Central Plain, uncommon and more localized in the Northern Highland. Breeding Bird Survey data (Table 8) suggest that in the Western Upland and Central Plain the savannah sparrow is among the three most common nesting sparrows. However, this abundance decreases rapidly moving northward into the heavily forested Northern Highland.

Habitat: Characteristic breeding species of various grassland communities. Important among these are retired cropland, Old Field Community, highway rights-of-way, Managed Grasslands maintained for duck production, and lightly to moderately grazed tame pasture that is predominantly timothy or Kentucky bluegrass. Also important, although to a lesser degree, are alfalfa and oat fields. In Northern regions, savannah sparrows make extensive use of wet meadow habitats, primarily Northern Sedge Meadow.

Grasshopper Sparrow (*Ammodramus savannarum*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Western Upland and Central Plain, uncommon to rare and localized in the Northern Highland. Spring migrants arrive in the Western Upland 25 April to 1 May and the Northern Highland about 5 May. Peak spring migration is difficult to determine, although it is widely distributed 5–15 May. During the fall, grasshopper sparrows are rarely encountered after the song period ceases about 1 August, but they are probably present until mid-September.

Nesting Season Distribution: Fairly common nesting species in the Western Upland and Central Plain, rare and local in the Northern Highland. Jackson (1943) did not record this sparrow during the 1919 nesting season in northwestern Wisconsin. Breeding Bird Survey data (Table 8) suggest that the breeding populations in the Western Upland and Central Plain occur in nearly equal abundance, becoming much smaller in the Northern Highland.

Habitat: Primarily a nesting species of various grassland communities. Important among these are retired croplands, unmowed highway rights-of-way, Managed Grasslands maintained for duck production, and lightly grazed tame pasture that is predominantly Kentucky bluegrass or timothy. Also important, although to lesser degrees, are alfalfa and oat fields. Occasional use is made of the drier portions of Shrub Carr wetlands and Northern Sedge Meadow.

Baird's Sparrow (*Ammodramus bairdii*)

Status: Hypothetical, two records.

Records: One bird was observed at Crex Meadows, Burnett County, on 12 May 1957 (Stone 1957). Goddard (1976) reported a single bird, also at Crex Meadows, on 2 May 1975.

Le Conte's Sparrow (*Ammospiza leconteii*)

Status: Regular migrant and summer resident.

Migration: Rare migrant throughout the Valley, fairly common at Crex Meadows, Burnett County. Migrants arrive in the Western Upland about 5 May (earliest—24 April 1976, St. Croix County). LeConte's sparrow is most regularly observed 10–25 May. Fall migration records range from 3 September to 4 October (latest—11 October 1963, Burnett County).

Nesting Season Distribution: Green and Janssen (1975) show the breeding range of LeConte's sparrow extending throughout the three Minnesota counties. Although summer records exist for Burnett, Polk, and St. Croix counties, young have been observed only at Crex Meadows. The most southerly breeding season records include single birds near New Richmond, St. Croix County, on 15 June to 2 July 1964, and 16 June 1966 (Robbins 1969*b*), and a singing male near Roberts, St. Croix County, on 27 June 1977 (Sec. 32, T. 30 N., R. 18 W.). Robbins (1969*b*) also recorded LeConte's sparrow in two Polk County locations (T. 35 N., R. 16 W.) on 15 June 1968. Two late May records from Pine County (23 May 1970 and 29 May 1971) were probably of birds on breeding territory.

The best known and probably most extensively explored summer area for LeConte's sparrow is the Crex Meadows Wildlife Area, Burnett County. Southern (1962) found several LeConte's sparrows in the marshes at Crex Meadows between 23 June and 2 July 1959. Subsequent to his original observations, other birders have investigated this area extensively and have found that this species occurs commonly in proper habitat. On 10 June 1977, I recorded 11 singing males in one marsh at Crex Meadows (Sec. 15, T. 39 N., R. 18 W.). Frequency of occurrence and observations of apparent territorial behavior indicate that LeConte's sparrow still nests at Crex Meadows, although no nests have been obesrved recently. Intensive investigation of similar areas in Pine and southern Douglas counties should reveal additional breeding areas.

Habitat: Typical breeding habitat at Crex Meadows includes extensive stands of Northern Sedge Meadow characterized by manna grass, water sedge, bluejoint grass, rattlesnake grass, and dark-green bulrush. Breeding season records of this sparrow away from Crex Meadows have consisted of birds in drier upland grasses, primarily timothy, bromegrass, and Kentucky bluegrass.

Henslow's Sparrow (*Ammodramus henslowii*)

Status: Regular migrant and nesting species.

Migration: Rare migrant in the Western Upland and Central Plain. Spring migrants arrive in the Western Upland 25 April to 1 May. There is very little movement that could be considered peak spring migration. Most of the birds observed in the Valley appear to be on or near a nesting territory. A Henslow's sparrow was observed at Crex Meadows, Burnett County, on 15 May 1954. This is the only record for the Northern Highland. Fall migration is similar to spring in that no well-defined movements have been observed. Most fall observations have been made during August (latest—12 September 1977, St. Croix County).

Nesting Season Distribution: Rare and local nesting species, restricted primarily to the Western Upland and Central Plain (Table 8). The secretive behavior of Henslow's sparrow and its short and nondescript song make this bird one of the most difficult breeding birds in the Valley to observe.

Habitat: Restricted during the breeding season to several grassland communities. Primary use is made of retired agricultural fields that have developed a rank growth of vegetation, primarily timothy and various forbs. Managed Grasslands maintained for duck production provide important nesting habitat, especially when vegetation height exceeds 0.5 m. Occasional use is made of alfalfa fields and tame pastures or thick grassland vegetation associated with the periphery of seasonally and semipermanently flooded wetlands.

Sharp-tailed Sparrow (*Ammospiza caudacuta*)

Status: Casual migrant and summer resident.

Migration: Three spring and one fall migration records exist for the Valley including 19 May 1964, St. Croix County; 8 May 1974, Pierce County (Faanes and Goddard 1976); and 23 May 1976, Burnett County (Crex Meadows). One bird was observed in St. Croix County on 18 August 1977. Because of the secretive habits of this species, and its extremely high-pitched song, the sharp-tailed sparrow is probably more common than records indicate.

Nesting Season Distribution: The sharp-tailed sparrow has been recorded at Crex Meadows, Burnett County, on at least five occasions during the nesting season. The first record was of one singing male on 21–22 July 1969. On 31 July and 1 August 1970, one singing male was recorded in the same area. It was not until 13 August 1975 that T. C. Baptist again recorded this sparrow in the same marsh. Tessen (1978) reported observing at least three singing males on 28 and 29 May 1977. Later, on 10 June 1977, I recorded one singing male at the same location. All Crex Meadows observations during the breeding season were made in a large sedge meadow in Sec. 15, T. 39 N., R. 18 W. Because of the territorial behavior exhibited by these birds, sharp-tailed sparrows can be considered a probable breeding species at Crex Meadows.

Habitat: The area that sharp-tailed sparrows occupy at Crex Meadows is an extensive Northern Sedge Meadow that is characterized by manna grass, bluejoint grass, and water sedge. Although habitat similarities exist between sharp-tailed and LeConte's sparrow at Crex Meadows, apparently sharp-tailed sparrows choose moister areas in the meadow.

Vesper Sparrow (*Pooecetes gramineus*)

Status: Regular migrant and nesting species.

Migration: Common spring and fall migrant in the Western Upland and Central Plain, uncommon and more local in the Northern Highland. Spring migrants arrive in the Western Upland 5–10 April (earliest—25 March 1963, St. Croix County) and the Northern Highland 10–15 April. Peak spring migration through the Valley occurs 15 April to 1 May. Peak fall migration occurs 1–20 September and departure by 15 October.

Nesting Season Distribution: Common nesting species in the Western Upland and Central Plain, uncommon in the Northern Highland. Erickson (1937), however, considered it abundant in Pine County. Breeding Bird Survey data (Table 8) suggest that the vesper sparrow is the second most abundant nesting sparrow in the Valley. Jackson (1943) reported that the vesper sparrow was a common breeding bird throughout most of northwestern Wisconsin in 1919.

Habitat: Characteristic nesting species of edge situations including fencerows adjoining agricultural fields and the border of retired cropland with deciduous forest. Brushy highway rights-of-way and Old Field Communities are regularly used in the Western Upland and Central Plain. Breeding vesper sparrows in northern regions occur in open areas, brushy fields, or occasionally in openings in Jack Pine Barrens.

Lark Sparrow (*Chondestes grammacus*)

Status: Regular migrant and summer resident.

Migration: Rare spring and fall migrant in the Western Upland and Central Plain, absent from the Northern Highland except in the region near Grantsburg, Burnett County. Spring migration dates occur during a narrow range from 10–25 May. Fall migration dates range from 1–15 September.

Nesting Season Distribution: The only evidence of possible breeding in the Valley is available from the Union BBS transect in Burnett County. S. D. Robbins found a small breeding "colony" of lark sparrows near Grantsburg on 26 June 1975. Since then, up to five singing males have been recorded in that location each year, but no nests of young have yet been found. Green and Janssen (1975) showed that the breeding range of this sparrow in Minnesota includes Chisago, Washington, and southern Pine counties. S. D. Robbins (personal communication) observed lark sparrows near Cushing, Polk County, on 22 June 1977 and near North Hudson, St. Croix County, on 8 July 1965. During June 1977 I observed a group of five lark sparrows in St. Croix County (Sec. 22, T. 30 N., R. 18 W.). The appearance of two of these birds suggested that they were young of the year. Kemper (1973) considered this species rare in Chippewa and Eau Claire counties, 120 km east of the St. Croix County location.

Habitat: Lark sparrows at the Burnett County location use an open area in mixed bur oak–jack pine. The St. Croix County location was characterized by the brushy edge of a Managed Grassland.

Dark-eyed Junco (*Junco hyemalis*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant throughout the Valley. Determination of arrival of spring migrants in the Western Upland and Central Plain is confounded by wintering birds. The first noticeable influxes occur 1–15 March. First spring migrants arrive in the Northern Highland 15–30 March. Peak spring migration through the Valley occurs 30 March to 15 April and departure from nonbreeding areas by 15 May. Fall migration begins in the Northern Highland during early September. First migrants arrive in the Western Upland 15–25 September. Peak fall migration occurs during October and most nonwintering birds have departed by 1 December.

Nesting Season Distribution: Rare nesting species, restricted to the Northern Highland. Roberts (1932) reported young being fed in Pine County during late June 1918, the first breeding record for the Valley. Two young dark-eyed juncos were observed in Chisago County on 16 June 1950 (Warner 1951). Breeding Bird Survey data (Table 8) also suggest that the breeding population of this species is rather limited in the Valley. An adult that I observed near Deer Park, St. Croix County, on 23 June 1976 was extralimital and probably an extremely late migrant.

Winter: Common (locally abundant) winter resident along the lower St. Croix River in Pierce, St. Croix, and southern Washington counties. Rare and local in the Central Plain, occasional in the Northern Highland. Christmas Bird Count data (Table 4) show the rapid decrease in relative abundance of this species moving north through the Valley during the winter. Dark-eyed juncos are well known for their attachment to the numerous winter feeding stations in residential areas.

Habitat: Primarily a species of drier upland habitats including Jack Pine Barrens and mixed Northern Hardwood Forest. Roberts (1932) mentioned that nesting dark-eyed juncos are also associated with "spruce and cedar swamps of the lowlands" in Pine County. Wintering dark-eyed juncos make extensive use of edge habitats, particularly hedgerows, and to a lesser extent several deciduous forest types, primarily Southern Deciduous Forest and Lowland Deciduous Forest.

Tree Sparrow (*Spizella arborea*)

Status: Regular migrant and winter resident.

Migration: Abundant migrant throughout the Valley. Fall migrants arrive in the Northern Highland 5–10 October and in the Western Upland 10–15 October. Peak fall migration occurs 25 October to 25 November and departure of most nonwintering birds occurs by 30 November. Spring migrants arrive in the Northern Highland 1–10 April. Peak spring migration throughout the Valley occurs 10–20 April and departure by 30 April; occasional stragglers linger through 15 May.

Winter: Fairly common (locally common) winter resident in the Western Upland, rare and local in the Central Plain. Christmas Bird Count data (Table 4) suggest that highest winter populations occur in areas directly adjacent to the lower St. Croix River. Populations decrease rapidly in areas northward from the Central Plain. The tree sparrow has not been recorded on the Solon Springs CBC, Douglas County.

Habitat: During migration, the tree sparrow uses a variety of open habitats including agricultural fields, retired cropland, and wetland edges. During midwinter, extensive use is made of retired croplands that support dense weedy patches. Grassy openings in Southern Deciduous Forest and occasional remnant prairie patches occurring along the river bluffs are also important.

Chipping Sparrow (*Spizella passerina*)

Status: Regular migrant and nesting species.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 10–15 April (earliest—3 April 1971, Washington County) and reach the Northern Highland about 15–20 April. Peak spring migration through the Valley occurs 1–15 May. Peak fall migration occurs 10 September to 1 October and departure by 15 October (latest—3 November 1963, St. Croix County).

Nesting Season Distribution: Common nesting species throughout the Valley. Breeding Bird Survey data (Table 8) suggest that the largest breeding population occurs in the northern regions of the Central Plain and throughout the Northern Highland. Jackson (1943) reported that chipping sparrows were common nesting birds throughout northwestern Wisconsin. Goddard (1972) reported a density of 11.1 pairs per 40 ha in the Kinnickinnic River Valley, Pierce County.

Habitat: Primarily a nesting species of various coniferous habitats including Lowland Coniferous Forest, Black Spruce–Tamarack Bogs, and Jack Pine Barrens. In residential areas, this sparrow is common in ornamental shrubs. Breeding pairs are occasionally encountered in brushy margins between Lowland Deciduous Forest and open fields. Jackson (1943) described a chipping sparrow nest at St. Croix Falls that was 6.4 m above ground in a large white pine.

Clay-colored Sparrow (*Spizella pallida*)

Status: Regular migrant and nesting species.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 25 April to 1 May and the Northern Highland 5–10 May (earliest—29 April 1961, Burnett County). Peak spring migration through the Valley occurs 10–20 May. Peak fall migration occurs 20 August to 5 September in the Northern Highland and 10–25 September elsewhere. Departure from the Northern Highland occurs about 20 September (latest—16 October 1963, Burnett County) and the Western Upland 1–15 October.

Nesting Season Distribution: Fairly common and local nesting species in all regions, probably most abundant in the Northern Highland (Table 8). Jackson (1943) reported that the clay-colored sparrow was a common nesting species at Danbury (Burnett County) and Solon Springs (Douglas County) in 1919. Clay-colored sparrows apparently become semicolonial where habitat is favorable.

Habitat: Primarily a species of edge situations including brushy fields. This species becomes numerous in recently burned areas or where there are relatively young conifer plantings. Commonly found associated with retired agricultural fields and Old Field Community where coarse perennial weeds have become established. In the Northern Highland, this species has responded favorably to intensive management for sharp-tailed grouse on sandy soils. Nests are usually found in association with sweet fern vegetation in areas of restored native prairie. Nesting clay-colored sparrows near the mouth of the Kinnickinic River in Pierce and Washington counties are associated with brushy open areas in Southern Deciduous Forest.

Field Sparrow (*Spizella pusilla*)

Status: Regular migrant and nesting species, casual early winter resident.

Migration: Fairly common to common migrant throughout the Valley. Locally distributed in heavily forested regions of the Northern Highland. Spring migrants arrive in the Western Upland about 10–20 April and the Northern Highland by 1 May. Peak spring migration through the Valley occurs late April to 15 May. Fall migration begins in the northern regions in late August and departure is by 15 September. Peak fall migration through the lower Valley occurs during 15–25 September and departure by 15 October.

Nesting Season Distribution: Fairly common and well-distributed nesting species in the Western Upland and Central Plain. Rare (locally common) nesting species in the Northern Highland. Bernard (1967) considered this sparrow a rare summer visitor and possible resident in Douglas County. Breeding Bird Survey data (Table 8) suggest that the field sparrow occurs fairly regularly during the nesting season in southern Douglas County. Roberts (1932) credited the removal of coniferous forest and replacement with a deciduous forest type with the expansion of this sparrow northward along the St. Croix River to southern Pine County.

Winter: Three winter records for St. Croix County from the Afton CBC, including single birds on 1 January 1971 and 1973, and three birds in one group on 1 January 1978. It is not known if any of these birds survived the winter. When the location of the 1978 birds was rechecked on 12 January 1978, the birds were not found.

Habitat: Characteristic nesting species of the Old Field Community where it is associated with early successional species including box elder, trembling aspen, staghorn sumac, and chokecherry. Use is also made of well-established growths of various coarse weeds in retired agricultural fields. During early stages of development, field sparrows are regularly encountered in

Pine Plantations. Deciduous Clear Cuts and brushy openings in Jack Pine Barrens are used in the Northern Highland.

Harris' Sparrow (*Zonotrichia querula*)

Status: Regular migrant, one winter record.

Migration: Rare spring and uncommon fall migrant in the Western Upland and Central Plain, casual in the Northern Highland. Spring migrants arrive in the Western Upland 1-5 May and are most frequently observed 10-20 May, departing by 25 May. Fall migrants arrive 20 September to 1 October. Peak fall migration occurs 10-20 October and departure by 30 October (latest—2 November 1968, St. Croix County).

Winter: One bird was recorded on the Afton CBC (Washington County) on 1 January 1974 (Eckert 1974). On 4, 8, and 11 April 1967 S. D. Robbins observed one at Roberts, St. Croix County, that he suspected of overwintering somewhere in the area.

Habitat: Primarily a species of brushy edges of fields and hedgerows. Observations of Harris' sparrows indicate that they migrate in close association with white-crowned sparrows.

White-crowned Sparrow (*Zonotrichia leucophrys*)

Status: Regular migrant, one winter record.

Migration: Uncommon migrant throughout the Valley. Spring migrants arrive in the Western Upland 25 April to 1 May (earliest—2 April 1961, St. Croix County), reaching the Northern Highland 1-5 May (earliest—20 April 1954, Burnett County). Peak spring migration occurs 10-25 May and departure by 30 May (latest—11 June 1953, Burnett County; Besadny 1953). Fall migrants arrive 5-10 September. Peak fall migration occurs 15-20 September and departure 25 September to 10 October.

Winter: One white-crowned sparrow was observed at a feeder in Luck, Polk County, on 23 December 1957 (Lound and Lound 1958*b*).

Habitat: Edges of deciduous woods that support a brushy understory, brushy edges of retired agricultural fields, hedgerows, and ornamental plantings in residential areas.

White-throated Sparrow (*Zonotrichia albicollis*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant throughout the Valley. The white-throated sparrow is second only to the song sparrow in abundance during migration. Spring migrants arrive in the Western Upland 1-10 April and the Northern Highland by 15 April. Peak spring migration occurs 20 April to 10 May and departure from nonbreeding areas occurs by 25 May. Fall migration begins in the Northern Highland in late August and the first birds reach the Western Upland 5–10 September (earliest—25 August 1977, Pierce County). Peak fall migration occurs 15 September to 10 October. Departure from the Northern Highland occurs 10–20 October and elsewhere by 15 November.

Nesting Season Distribution: Common nesting species in the Northern Highland (Table 8), uncommon and local in the Central Plain. Green and Janssen (1975) showed that the breeding range of this sparrow extended south to the Chisago–Washington County line. My most southerly nest record was obtained on 9 June 1975, near Luck, Polk County (Sec. 19, T. 36 N., R. 17 W.).

Winter: Rare and regular winter resident in the Western Upland. Usually encountered each year on either the Afton or Suburban St. Paul CBC. One remained at St. Croix Falls, Polk County, during the 1949–50 Winter.

Habitat: The white-throated sparrow occupies both deciduous and coniferous habitats during the nesting season. There is no single habitat that can be considered characteristic. Deciduous habitats that are most regularly used include stands of mature Northern Hardwood Forest with sugar maple, basswood, and silver maple the predominant vegetation. Nests in this habitat are usually associated with lush grasses and forbs in the ground layer. Deciduous Clear Cuts <10 years old and predominantly trembling aspen with scattered patches of black raspberry are an important deciduous habitat. Coniferous habitats of major importance include Lowland Coniferous Forest dominated by yellow birch, white cedar, black spruce, and balsam fir. Extensive use is also made of Black Spruce–Tamarack Bogs. Use of Jack Pine Barrens is very low and irregular.

Fox Sparrow (*Passerella iliaca*)

Status: Regular migrant, casual early winter resident.

Migration: Fairly common migrant throughout the Valley. Spring migrants arrive in the Western Upland 15–25 March and the Northern Highland 1–5 April. Peak spring migration occurs 10–25 April and departure by 15 May (latest—28 May 1972, Washington County). Fall migrants arrive 10–15 September, peak fall migration occurs 1–20 October, and departure is by 15 November.

Winter: There are several early winter records from the Western Upland. These records include 13 December 1968, Chisago County, and 2 January 1960, 1 January 1970, 1974, and 1976 on the Afton CBC, Washington County.

Habitat: In the Western Upland, the fox sparrow is primarily a species of Southern Deciduous Forest characterized by white, Hill's, and bur oak. Extensive areas of brushy understory, primarily prickly ash, hazelnut, and beaked hazel are important components of that habitat. In the northern regions, fox sparrows use brushy edges and heavy undergrowth in Northern Hardwood Forest, primarily quaking aspen, sugar maple, basswood, white birch, and green ash.

Lincoln's Sparrow (*Melospiza lincolnii*)

Status: Regular migrant and possible summer resident.

Migration: Uncommon spring and fairly common fall migrant throughout the Valley, locally common in the Northern Highland. Spring migrants arrive in the Western Upland 1-5 May and the Northern Highland 5-10 May. Peak spring migration through the Valley occurs 10-20 May and departure 25 May to 1 June. Fall migration begins in the Northern Highland about 15 August with the first arrivals in the Western Upland 20-25 August. Peak fall migration occurs 15 September to 10 October and departure by 15-20 October (latest—28 October 1963, St. Croix County).

Nesting Season Distribution: S. D. Robbins (personal communication) recorded single Lincoln's sparrows along the route of the Minong BBS (Douglas County) on 16 June 1971 and 27 June 1975. On 26 June 1974 Robbins recorded one in an open bog about 6.4 km north of Moose Junction, Douglas County.

Habitat: Migrant Lincoln's sparrows are usually associated with brushy edge habitats. Old Field Community, retired agricultural fields, and ornamental shrubbery in residential areas are important among these. In the Northern Highland, this sparrow is regularly encountered in wet coniferous habitats, brushy borders of Northern Sedge Meadow, and in Alder Thickets.

Swamp Sparrow (*Melospiza georgiana*)

Status: Regular migrant and nesting species, one winter record.

Migration: Common migrant throughout the Valley. Spring migrants arrive in the Western Upland 25 March to 5 April and the Northern Highland 15-20 April. Peak spring migration through the Valley occurs 20 April to 5 May. Peak fall migration occurs 15 September to 10 October and departure by 20 October.

Nesting Season Distribution: Uncommon to fairly common nesting species in the Central Plain and Northern Highland, locally in the Western Upland. Jackson (1943) found the swamp sparrow "never particularly common" during the 1919 nesting season. He found nests with young at St. Croix Falls (Polk County) and Solon Springs (Douglas County). Breeding Bird Survey data (Table 8) suggest that the swamp sparrow is more abundant during the nesting season in the northern regions of the Central Plain and throughout the Northern Highland.

Winter: A single bird was observed in St. Croix County during the Afton CBC on 1 January 1970.

Habitat: Characteristic nesting species of Alder Thicket and Northern Sedge Meadow habitats in northern regions. Also fairly regular in Black Spruce-Tamarack Bogs and in open leatherleaf-Labrador tea bogs. In the Central Plain, this sparrow breeds regularly in Shrub Carr habitat which is dominated by heavy growths of gray dogwood and in cattail-bulrush vegetation associated with seasonally, semipermanently, and permanently flooded wetlands.

Song Sparrow (*Melospiza melodia*)

Status: Regular migrant, nesting species, and winter resident.

Migration: Abundant migrant throughout the Valley. Spring migrants arrive in the Western Upland 20 March to 1 April and the Northern Highland 1–10 April (earliest—13 March 1954, Burnett County). Peak spring migration occurs 15 April to 1 May. Peak fall migration is 1–10 September in the Northern Highland and 25 September to 10 October in the Western Upland. Departure from the Northern Highland occurs 15–25 October (latest—16 November 1975, Burnett County) and elsewhere by 5 November.

Nesting Season Distribution: Common nesting species throughout the Valley. Breeding Bird Survey data (Table 8) suggest that the song sparrow is the most abundant breeding sparrow in the Valley. Jackson (1943) reported that the song sparrow was a common nesting bird "at every locality visited" in northwestern Wisconsin in 1919. Goddard (1972) reported a breeding density of 40.3 pairs per 40 ha in the lower Kinnickinnic River Valley, Pierce County. Goddard also reported that the song sparrow was the second most abundant breeding bird among 82 species nesting in that valley.

Winter: Regularly occurring species during winter along the lower St. Croix River. Most birds are associated with feeding stations in residential areas.

Habitat: Nearly unrestricted in nesting habitat use. Important habitats are Shrub Carr, Alder Thicket, Prairie Wetlands, retired agricultural fields, Old Field Community, highway rights-of-way, and brushy openings in upland deciduous forest. Coniferous habitats are used to a lesser degree. Important among these are Black Spruce–Tamarack Bog and Lowland Coniferous Forest.

Lapland Longspur (*Calcarius lapponicus*)

Status: Regular migrant and winter resident.

Migration: Abundant migrant in the Western Upland, Central Plain, and unforested regions of the Northern Highland; rare in the heavily forested regions of the Northern Highland. Fall migrants arrive in the Northern Highland 15–20 September and the Western Upland 25 September to 1 October. Peak fall migration occurs 15 October to 15 November and most have departed by 1 December. Spring migrants arrive in the Western Upland 1–5 March and the Northern Highland about 15 March. Peak spring migration occurs 20 March to 10 April and departure by 10 May.

Habitat: An open country bird using primarily heavily grazed tame pasture, fall plowed agricultural fields, corn and oat stubble, and the exposed edges of Prairie Wetlands.

Winter: Uncommon winter resident of the Western Upland and Central

Plain, usually absent north of St. Croix Falls. Normal winter flock size is 10-30. The largest daily total on a CBC (Afton) is 174 on 1 January 1968.

Chestnut-collared Longspur (*Calcarius ornatus*)

Status: Accidental, one record.

Record: K. H. Dueholm observed three chestnut-collared longspurs in a flock of lapland longspurs on 20 March 1976, 4.8 km north of Star Prairie, Polk County.

Snow Bunting (*Plectrophenax nivalis*)

Status: Regular migrant and winter resident.

Migration: Common (locally abundant) migrant in the Western Upland, Central Plain, and unforested regions of the Northern Highland. Fall migrants arrive in the Northern Highland 10-20 October (earliest—5 October 1952, Burnett County) and the Western Upland 20-30 October. Peak fall migration occurs 10 November to 1 December. Peak spring migration occurs 1-15 March and departure by 15 April (latest—30 April 1971, Burnett County).

Winter: Fairly common (locally common) winter resident in the unforested areas of the Valley. Christmas Bird Count data suggest that largest numbers occur in the Central Plain and Northern Highland. The largest group on record (2,500) was recorded by N. R. Stone at Crex Meadows, Burnett County, on 21 December 1950.

Habitat: Primarily a species of open country using heavily grazed tame pasture, fall plowed agricultural fields, and corn or oat stubble. In the Northern Highland, occasional use is made of grassy railroad rights-of-way that traverse extensive hardwood forest stands.

Acknowledgments

This report has been greatly enhanced by the observations and contributions of many birders and ornithologists too numerous to mention individually. The entire manuscript benefited from critical reviews by D. R. Bystrak, J. C. Green, C. S. Robbins, S. D. Robbins, and D. D. Tessen. Individual sections of the manuscript were critically reviewed by B. A. Moss (waterfowl), K. H. Dueholm, and J. W. Richardson (habitats). Additional suggestions and comments on various portions of the manuscript were provided by H. F. Duebbert, C. L. Henderson, R. L. Hine, D. H. Johnson, H. A. Kantrud, and R. L. Kologiski. Publication of these data was originally proposed by E. Lanis.

The staff of the Northern Prairie Wildlife Research Center contributed in many ways. R. L. Duval and C. W. Shaiffer prepared the figures. E. K. Bartels provided extensive bibliographic support.

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Appendix A

Common and Scientific Names of Plants Mentioned in Text

Species	Scientific name
Alfalfa	*Medicago sativa*
American elm	*Ulmus americana*
Arrowhead	*Sagittaria latifolia*
Awned sedge	*Carex atherodes*
Awnless bromegrass	*Bromus brizaeformis*
Balsam fir	*Abies balsamea*
Barley	*Hordeum vulgare*
Basswood	*Tilia americana*
Beaked hazel	*Corylus cornuta*
Bearberry	*Arctostaphylos uva-ursi*
Big bluestem	*Andropogon gerardi*
Big-leaf aster	*Aster macrophyllus*
Bindweed	*Convolvulus sepium*
Bishop's cap	*Mitella diphylla*
Black ash	*Fraxinus nigra*
Black cherry	*Prunus serotina*
Black raspberry	*Rubus occidentalis*
Black spruce	*Picea mariana*
Black willow	*Salix nigra*
Bladderwort	*Utricularia vulgaris*
Bloodroot	*Sanguinaria canadensis*
Blue bead lily	*Clintonia borealis*
Blue cohosh	*Caulophyllum thalictroides*
Blue vervain	*Verbena hasta*
Blueberry	*Vaccinium angustifolium*
Bluejoint grass	*Calamogrostis canadensis*
Bog birch	*Betula glandulosa*
Bog laurel	*Kalmia polifolia*
Bog rosemary	*Andromeda glaucophylla*
Bottle-brush grass	*Hystrix patula*
Box-elder	*Acer negundo*
Bracken fern	*Pteridium aquilinum*
Bristly sedge	*Carex comosa*
Brome grass	*Bromus* spp.
Brown sedge	*Carex buxbaumii*
Buckbean	*Menyanthes trifoliata*
Bunchberry	*Cornus canadensis*
Bur oak	*Quercus macrocarpa*
Burreed	*Sparganium eurycarpum*
Canada bluegrass	*Poa compressa*
Canada mayflower	*Maianthemum canadense*

Species	Scientific Name
Cane reed	*Phragmites communis*
Cattail	*Typha latifolia*
Choke cherry	*Prunus virginiana*
Common elder	*Sambucus canadensis*
Common milkweed	*Aesclepias syriaca*
Coontail	*Ceratophyllum demersum*
Corn	*Zea mays*
Cottongrass	*Eriophorum angustifolium*
Cottonwood	*Populus deltoides*
Creeping snowberry	*Gaultheria hispidula*
Crested sedge	*Carex cristatella*
Daisy fleabane	*Erigeron strigosus*
Dark-green bulrush	*Scirpus atrovirens*
Dogbane	*Apocynum androsaemifolium*
Downy yellow violet	*Viola pubescens*
Dwarf ginseng	*Panax trifolium*
Elodea	*Anacharis nuttallii*
Evening primrose	*Oenothera biennis*
False Solomon's seal	*Smilacina stellata*
Field mint	*Mentha arvensis*
Flowering crab apple	*Pyrus* spp.
Flowering spurge	*Euphorbia corollata*
Fox sedge	*Carex vulpinoidea*
Foxtail sedge	*Carex alopecoidea*
Germander	*Teucrium canadense*
Goat's beard	*Tragopogon pratensis*
Goosegrass	*Galium aparine*
Gray dogwood	*Cornus racemosa*
Great water dock	*Rumex altissimus*
Green ash	*Fraxinus pennsylvanica*
Ground pine	*Lycopodium clavatum*
Hardstem bulrush	*Scirpus acutus*
Hawthorn	*Crategus* spp.
Hazelnut	*Corylus americana*
Hedge nettle	*Stachys tenuifolia*
Hemlock	*Tsuga canadensis*
Hill's oak	*Quercus hillii*
Hoary alyssum	*Berteroa incana*
Indian pipe	*Monotropa uniflora*
Inland sedge	*Carex interior*
Intermediate wheatgrass	*Agropyron intermedium*
Iris	*Iris versicolor*
Ironwood	*Ostrya virginiana*
Jack-in-the-pulpit	*Arisaema atrorubens*
Jack pine	*Pinus banksiana*
Jacob's ladder	*Polemonium repens*
Jewelweed	*Impatiens biflora*

Species	Scientific name
Kentucky bluegrass	*Poa pratensis*
Labrador tea	*Ledum groenlandicum*
Large-flowered trillium	*Trillium grandiflorum*
Large-toothed aspen	*Populus grandidentata*
Leatherleaf	*Chamaedaphne calyculata*
Little bluestem	*Andropogon scoparius*
Manna grass	*Glyceria canadensis*
Marsh bellflower	*Campanula aparinoides*
Marsh cinquefoil	*Potentilla palustris*
Marsh milkweed	*Asclepias syriaca*
Marsh shield fern	*Dryopteris thelypteris*
Meadowsweet	*Spirea alba*
Moth mullein	*Verbascum blattaria*
Mountain ash	*Sorbus americana*
Mountain holly	*Nemopanthus mucronata*
New Jersey tea	*Ceanothus ovatus*
Noble goldenrod	*Salidago speciosa*
Northern bedstraw	*Galium boreale*
Oats	*Avena sativa*
Partridge berry	*Mitchella repens*
Pearly everlasting	*Anaphalis margaritacea*
Pennsylvania sedge	*Carex pennsylvanica*
Pickerelweed	*Pontederia cordata*
Pitcher plant	*Sarracenia purpurea*
Poison ivy	*Toxicodendron radicans*
Prickly ash	*Xanthoxylum americanum*
Purple-stem aster	*Aster puniceus*
Quack grass	*Agropyron repens*
Ragweed	*Ambrosia* spp.
Rattlesnake fern	*Botrychium virginianum*
Rattlesnake grass	*Glyceria canadensis*
Red clover	*Trifolium pratense*
Red maple	*Acer rubrum*
Red oak (Northern)	*Quercus borealis*
Red-osier dogwood	*Cornus stolonifera*
Red pine	*Pinus resinosa*
Reed canary grass	*Phalaris arundinacea*
Rice grass	*Oryzopsis asperifolia*
River bulrush	*Scirpus fluviatilis*
Round-leaf sundew	*Drosera rotundifolia*
Scotch pine	*Pinus banksiana*
Sharp-toothed goldenrod	*Solidago juncea*
Sheep sorrel	*Rumex acetosella*
Silver maple	*Acer saccharinum*
Silver willow	*Salix discolor*
Skunk cabbage	*Symplocarpus foetidus*
Slender sedge	*Carex lasiocarpa*

Species	Scientific Name
Small bedstraw	*Galium trifidum*
Softstem bulrush	*Scirpus validus*
Solomon's seal	*Polygonatum biflorum*
Soybean	*Glycine max*
Speckled alder	*Alnus rugosa*
Sphagnum moss	*Sphagnum* spp.
Spikerush	*Eleocharis* spp.
Spotted joe-pye weed	*Eupatorium maculatum*
Staghorn sumac	*Rhus typhina*
Starflower	*Trientalis borealis*
Sugar maple	*Acer saccharum*
Sweet cicely (Jarvil)	*Osmorhiza claytoni*
Sweet fern	*Comptonia peregrina*
Switchgrass	*Panicum virgatum*
Tall manna grass	*Glyceria grandis*
Tamarack	*Larix laricinia*
Tartarian honeysuckle	*Lonicera tartarica*
Tick trefoil	*Desmodium glutinosum*
Timothy	*Phleum pratensis*
Toothwort	*Dentaria laciniata*
Trembling aspen	*Populus tremuloides*
Turtlehead	*Chelone glabra*
Tussock sedge	*Carex stricta*
Twisted stalk (Rose mandarin)	*Streptopus roseus*
Virginia strawberry	*Fragaria virginiana*
Virginia waterleaf	*Hydrophyllum virginicum*
Water horehound	*Lycopus virginicus*
Water milfoil	*Myriophyllum* spp.
Water plaintain	*Alisma plantago-aquatica*
Water sedge	*Carex aquatilis*
Wheat	*Triticum aestivuum*
White ash	*Fraxinus americana*
White birch	*Betula papyrifera*
White cedar	*Chamaecyparis thyoides*
White oak	*Quercus alba*
White pine	*Pinus strobus*
White spruce	*Picea glauca*
White waterlily	*Nymphaea tuberosa*
Whorled loosestrife	*Lysimachia quadrifolia*
Wild cranberry	*Vaccinium macrocarpon*
Wild cranesbill	*Geranium maculatum*
Wild leek	*Allium tricoccum*
Wild lettuce	*Lactuca canadensis*
Wild rice	*Zizania aquatica*
Wild sarsaparilla	*Aralia nudicaulis*
Wintergreen	*Gaultheria procumbens*

Species	Scientific Name
Wood anemone	*Anemone quinquefolia*
Wood nettle	*Laportea canadensis*
Yarrow	*Achillea millefolium*
Yellow birch	*Betula alleghaniensis*
Yellow waterlily	*Nuphar variegatum*
Yellowish sedge	*Carex abacta*

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*U.S. GOVERNMENT PRINTING OFFICE : 1984 0-432-925/4402

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March 3, 1849

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
EDITORIAL OFFICE
AYLESWORTH HALL, CSU
FORT COLLINS, COLORADO 80523

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ECOLOGY AND BIOLOGY OF THE PACIFIC WALRUS, *ODOBENUS ROSMARUS DIVERGENS* ILLIGER

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Library of Congress Cataloging in Publication Data

Fay, Francis H.
Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger.

(North American fauna ; no. 74)
Bibliography: p.
1. Walruses. I. Title. II. Title: Pacific walrus, Odobenus rosmarus divergens. III. Series.
QL737.P62F38 599.74'7 81-15265
AACR2

NOTE: Use of trade names does not imply U.S. Government endorsement of commercial products.

ECOLOGY AND BIOLOGY OF THE PACIFIC WALRUS, *ODOBENUS ROSMARUS DIVERGENS* ILLIGER

by

Francis H. Fay

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
North American Fauna, Number 74

Washington, D.C. • 1982

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Frontispiece. Bull walruses in agonistic encounter involving tusk display. (Photo by J. W. Brooks)

Ecology and Biology of the Pacific Walrus, *Odobenus rosmarus divergens* Illiger

by

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Abstract

The distribution, physical development, pelage, dentition, feeding behavior, reproduction, causes of mortality, and population structure of the Pacific walrus (*Odobenus rosmarus divergens*) were studied intermittently from 1952 to 1979. In winter, these animals tend to concentrate in north-central and southeastern Bering Sea, where sea ice conditions are most favorable for them. In summer, they concentrate mainly in northwestern and northeastern Chukchi Sea, along the edge of the ice. Most of the northward migrants are females and young; a large proportion of the adult males remains in the Bering Sea throughout the summer. Pacific walruses show strong sexual dimorphism; adult males are about 18% longer and 45% heavier and tend to have larger, more divergent tusks, as well as thicker, lighter-colored, and less hairy skin than adult females. As in other sexually dimorphic otarioid pinnipeds, males undergo secondary growth, beginning about the time of puberty and ending in full physical maturity about 15 years of age. The first pelage is a fine, white lanugo, which develops and is shed in utero. The second (natal) pelage, which resembles that of the adult, is shed and replaced 2 to 3 months after birth, in synchrony with the molt of older animals. The full primary and secondary dentitions include 38 and 30 teeth, respectively; 7 pairs of primary and 6 pairs of secondary teeth occur in less than 50% of the animals. The permanent first upper premolar is a secondary tooth, preceded by an uncalcified primary tooth. The lower premolars appear to be homologues of $P_{2\text{-}3\text{-}4}$, rather than $P_{1\text{-}2\text{-}3}$. The cheek teeth grow in length very slowly, and the pattern of decrement of their crowns indicates no contact with molluscan shells except in the incisive area at the front of the mouth. The abrasion of the tusks indicates that they are dragged through the bottom sediments, rather than used for digging or raking. Food of the Pacific walrus consists of more than 60 genera of marine organisms, most of which are situated on or just beneath the surface of the sediments. The walrus apparently locates these tactually with its sensitive mystacial vibrissae and by "rooting" with its snout. Soft-bodied organisms are ingested directly, without mastication; the soft parts (siphon, foot) of mollusks probably are separated from the shells by suction. The intake of food is at least 5 to 7% of the total body weight per day. Most females ovulate for the first time at 5 or 6 years; males become fertile at 8 to 10 years but probably do not participate in mating until fully mature at 15 years. Walruses are polygynous; mating takes place mainly in mid-winter. Implantation of the blastocyst takes place about 5 months later, and the calf is born in the following spring, after a pregnancy lasting at least 15 months. Females tend to breed at 2-year intervals or less often and are most productive between the ages of 8 and 15 years. The principal causes of mortality appear to be predation, intraspecific trauma, and microbiological infections. The Pacific walrus population was severely depleted in the late 19th century and again in the mid-20th century by overharvests for commercial purposes. Over the past 20 years, it apparently has recovered rapidly, in response to reduced harvest. The sex ratio of breeding adults appears to be about 1 male:3 or 4 females. The crude birth rate in recent years is estimated at 17 ± 2%, and the survival of young to puberty appears to be very high.

Introduction

One of the most remarkable creatures in the Arctic is the walrus (*Odobenus rosmarus*), whose very existence and natural history were cloaked in mysticism and anthropomorphism until the 19th century (Gray 1853; Allen 1880; Cammann 1954). For thousands of years, this mammal was regarded by Eskimos and other native people of the North as having supernatural powers and human attributes. At the same time it was for them a natural resource of major importance. From the walrus they obtained food and fuel, as well as materials for making tools, shelters, boats, sleds, and clothing. In all probability, the harvesting of walruses by these indigenous people before the 18th century had little impact on the populations. The primitive hunter was not equipped to kill great numbers of these animals and had no incentive to take more than were required to meet his own daily needs.

A new era of exploitation of walruses and other animal resources of the northern seas was heralded in the North Pacific region by the arrival of European man in the 17th century. Finding rich, untapped resources in the Bering Sea, he came later in capacious ships and with the firearms and the economic incentive to take all that he could obtain. He did so for the next two centuries, as though the supply were endless (Fay 1957). From the Pacific walrus (*O. r. divergens*), the principal commodities taken were ivory, oil, and hides.

By the end of the 19th century, the walrus population was severely depleted, and in 1951 when my study was conceived, there seemed to be no indications of its being restored. Although commercial harvesting of walruses by American industries had all but ceased more than 35 years earlier, there were suggestions of continued decline of the population. That trend was reversed a decade later, but at the time when I began my work, the Pacific walrus appeared to be on the road to extinction. My primary goals then were to assess the status of the population and to identify the forces that were suppressing it. Of necessity, much of my emphasis was placed on supportive studies of the biology and ecology of this mammal. There was a dearth of such information in the literature at that time. The results of my work, up to 1979, make up the bulk of this report. Relevant published and unpublished information from other sources up to December 1978 has been included. This publication is not, however, an attempt to review all available information.

I began my field work in April 1952 in the Eskimo village of Gambell (*Sevúokak*) on the northwestern tip of St. Lawrence Island (Fig. 1). I chose that

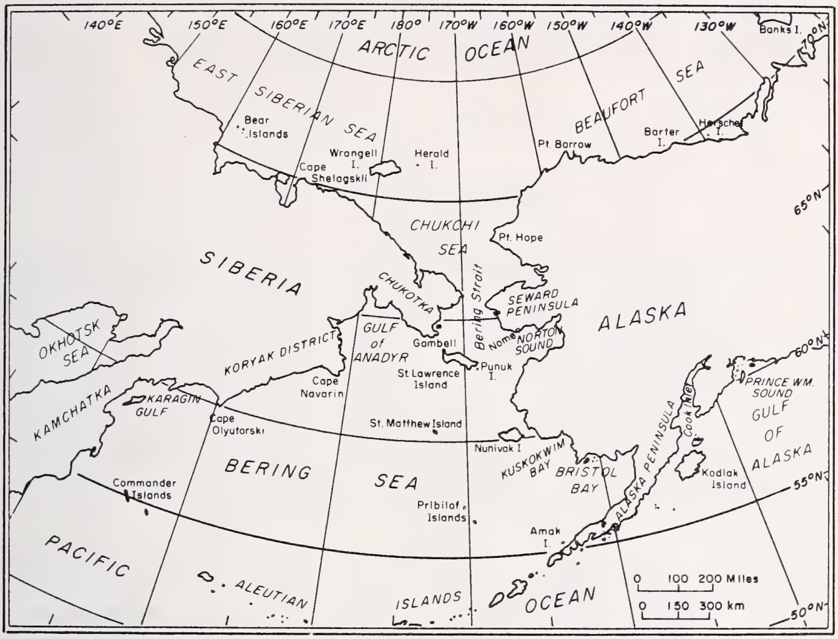

Fig. 1. Bering–Chukchi region, showing the principal places mentioned in the text.

site because (1) it was recognized as one of the four major walrus-harvesting villages in Alaska, and (2) it was the only one to which reliable air transportation was available at that time. Concurrently, James W. Brooks began similar work on Little Diomede Island in Bering Strait and at the village of Barrow on the northern coast of Alaska. A year later, Brooks reviewed the general status of the walrus population as revealed by his investigations and related it to existing social, economic, and management problems in western and northern Alaska (Brooks 1953). The full results of his work were produced in the following year as a special report of the Alaska Cooperative Wildlife Research Unit (Brooks 1954).

I continued my work at Gambell in 1953 and 1954 and on a part-time, opportunistic basis there and in other localities thereafter. At the same time, Soviet and American biologists, notably V. I. Krylov, V. N. Gol'tsev, K. W. Kenyon, and J. J. Burns, connected with Federal and State management agencies, intensified their work, and the scope of investigations was greatly broadened. Many important questions still remain unanswered. Growing public concern for the welfare of marine mammals of the world, together with concerns about their competitive position with commercial fisheries and their potential vulnerability to environmental disturbances, demand that the major gaps be promptly filled.

The following account is mainly descriptive. In it, I have considered aspects of the distribution and migrations of the Pacific walrus population, the developmental characteristics of individuals, their food and feeding, reproduction, mortality, and finally, my views on the history and current status of the population.

Systematics and Taxonomy

The seals, sea lions, and walruses of the world have been regarded for a long time as constituting a single order or suborder of carnivorous mammals, known as the Pinnipedia Illiger, 1811. Each of these subgroups of pinnipeds bears superficial resemblance to the others in the possession of a fusiform body and, as the name signifies, webbed, fin-like appendages. The proximal half or more of each limb is enclosed in the relatively thick skin-envelope of the body; ear pinnae are mostly absent or greatly reduced; a thick layer of fat (blubber) underlies the skin; and the adult pelage of all but the fur seals generally is more short, coarse, and sparse than that of their terrestrial relatives, the fissiped carnivores (Scheffer 1958, 1964).

The possibility of derivation of the Pinnipedia from more than one line of ancestral canoid carnivores has long been debated (e.g., see McLaren 1960) and now seems virtually certain (Tedford 1976). Hence, a new classification has been proposed, which takes into consideration these newly recognized relationships (Tedford 1976:372; Repenning and Tedford 1977:8). For the living pinnipeds, this classification is as follows:

- Order CARNIVORA Bowdich, 1821
  - Suborder Caniformia Kretzoi, 1943
    - Superfamily Otarioidea Gill, 1866
      - Family Otariidae Gill, 1866 (fur seals and sea lions)
      - Family Odobenidae Allen, 1880 (walruses)
    - Superfamily Musteloidea Swainson, 1835
      - Family Phocidae Gray, 1825 (hair seals)

Repenning and Tedford (1977) have traced the Odobenidae to a common origin with the Otariidae in the early Miocene, some 20 million years ago (Fig. 2), from an aquatic ancestral group (Enaliarctidae Mitchell and Tedford, 1973) having close affinity to primitive ursine (bear-like) carnivores. Those origins were in the North Pacific Ocean, whereas it seems likely that the hair seals or Phocidae were derived somewhat earlier from an otter-like ancestor, probably in the European sector of the North Atlantic Ocean (Ray 1976). The primitive walrus-like pinnipeds evidently flourished and became greatly diversified in late Miocene–early Pliocene times, but only one form has survived to the present, the living walrus, *Odobenus rosmarus* Linnaeus, 1758. The ancestor of this form apparently made its way from the Pacific to the Atlantic via the Central American Seaway between 5 and 8 million years ago; some time later, the Pacific stock(s) became extinct. The modern walruses of the North Pacific region were derived from the Atlantic stock, having made their way back to the Pacific via the Arctic Ocean sometime within the last million years (Repenning 1976).

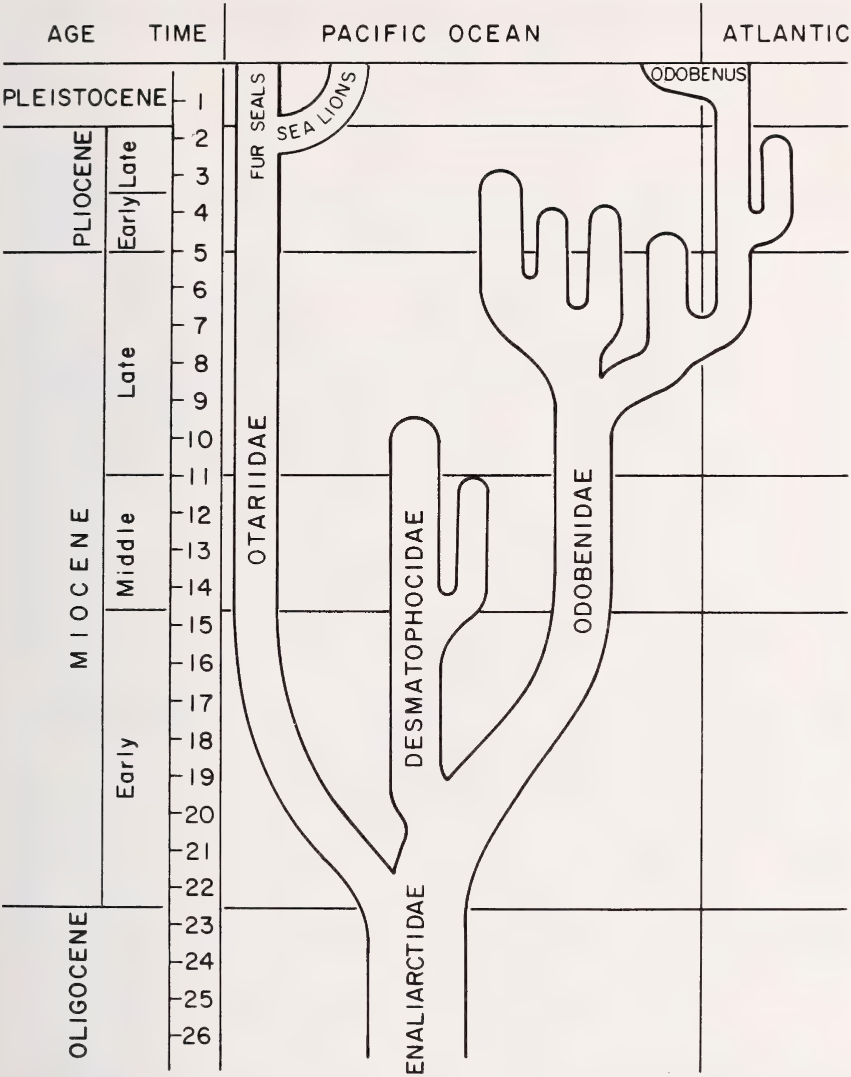

Fig. 2. Family tree of the otarioid pinnipeds. (Adapted from Repenning and Tedford 1977)

The single species of living walrus, *Odobenus rosmarus*, is holarctic in distribution, though by no means uniformly distributed or morphologically alike in all areas. At least six populations around the Northern Hemisphere appear to be geographically isolated at present (Fig. 3) in the (1) Hudson Bay–Davis Strait region, (2) eastern Greenland, (3) Svalbard and Franz Josef Land, (4) Kara Sea–Novaya Zemlya, (5) Laptev Sea, and (6) Bering and Chukchi seas. Of these, the first four are regarded as "the Atlantic walrus," *O. r. rosmarus* Linnaeus,

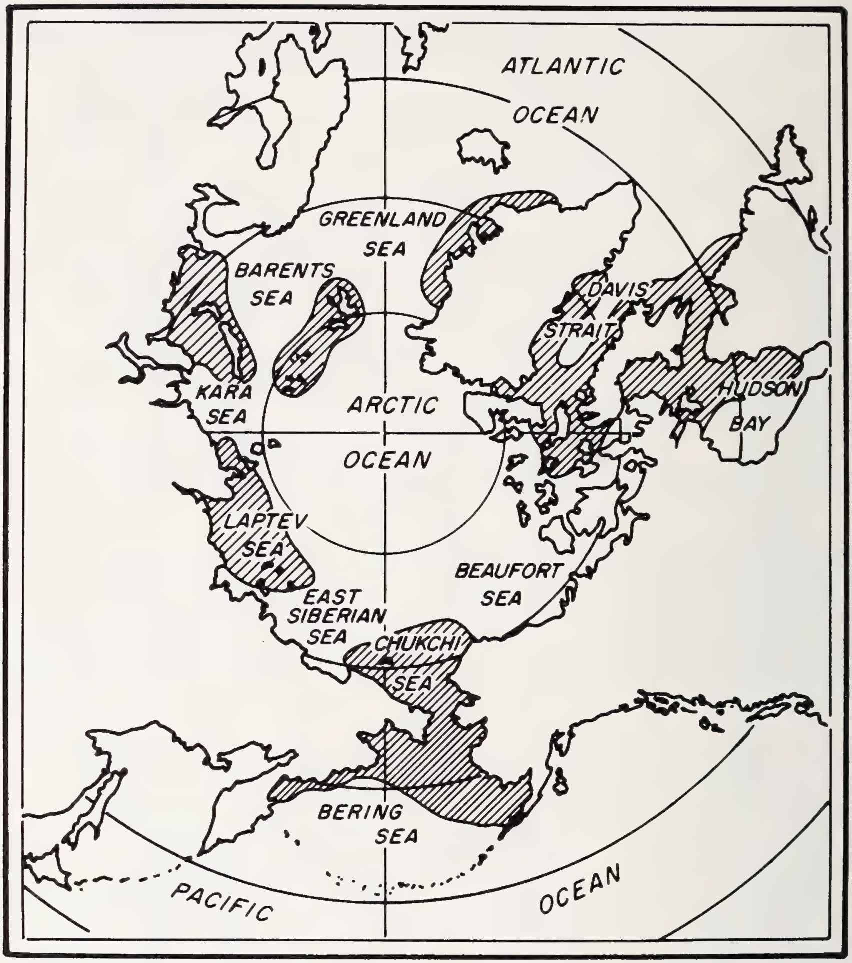

Fig. 3. Current world distribution of walruses.

1758, and the sixth as "the Pacific walrus," *O. r. divergens* Illiger, 1811. The taxonomic status of the population in the Laptev Sea is uncertain. It has been included by some workers in the Atlantic subspecies and by others in the Pacific subspecies. It is regarded by a few biologists in the Soviet Union as a third subspecies, *O. r. laptevi* Chapskii, 1940. For the sake of convenience in this report, I exclude the Laptev walrus from *O. r. divergens*, although I feel that its strongest affinities lie there.

The Pacific walrus differs from those of the North Atlantic region principally in size, being larger of body than any others (including the Laptev form) and having relatively much larger tusks (Heptner et al. 1976). Apparently, it differs also in having a broader, more "square" snout (as opposed to a narrower, more sloping snout) and much greater "lumpiness" of the skin on the neck and shoulders of the adult males (Allen 1880; Pedersen 1962). Probably, there are other differences that have not yet been recognized.

Distribution and Migrations

Nearly the entire life of the Pacific walrus is spent at sea, though perhaps no more than two-thirds of it is spent in the water (Fay and Ray 1968). Walruses frequently come out of the water (haul out) onto ice or land to rest and, in certain seasons, to bear their young and to molt. The usual place for hauling out is on snow-covered ice floes, rather than on land, apparently by preference (Nikulin 1947). Keeping mainly to the moving pack ice, most of the population spends the winter in the Bering Sea and the summer in the Chukchi Sea. The regularity of the migrations northward in spring and southward in autumn must have been evident to Eskimos of the Bering Strait region for thousands of years.

The pattern of those migrations is known only in a general way from compilation of reports of sightings from land, from icebreaking ships, and from aircraft. The first major attempt to analyze and describe that pattern was by Belopol'skii (1939), based mainly on his observations in eastern Chukotka. A considerable volume of additional sightings from other locations was added by Nikulin (1941), who spent five summers with the Soviet sealing fleet in the Far East. Brooks (1954) and Burns (1965) briefly redescribed the migrations on the basis of the Soviet data and their own observations in the Bering Strait region and northward to Barrow.

A large amount of new data has become available in the years since Brooks' and Burns' reports were prepared. Both the United States and the Soviet Union have conducted numerous aerial surveys of the walrus' habitat since 1958, in efforts mainly to assess the numerical status of the population. Research expeditions into the habitat of the walrus via iceworthy vessels also have been more numerous. Thus, the information now available provides a much clearer view of the movements of the population than was available in the 1950's, when I began my work. However, as will be seen, some major gaps in our knowledge of annual movements still exist, mainly for the autumn and winter months and during the spring migration. It is not likely that all of those gaps will be filled very quickly, for the short daylight in winter and inclement weather in autumn interfere with aerial and shipboard observation.

I have summarized the data available to me concerning positions and numbers of walruses sighted in each month. These sightings were compiled from published records from 1930 to 1978 and from unpublished records up to 1979. These span a 50-year period in which the population apparently changed from a high to a very low number, then back to a high number again. The greater part of the sightings were recorded during the latter half of that period.

My sources of published records were Chechulin (1936), Belopol'skii (1939), Collins (1940), Freiman (1941), Nikulin (1941, 1947), Wilke (1942), Porsild (1945), Lantis (1946), Rainey (1947), Brooks (1953, 1954), Fay (1957), Manville (1961), Fedoseev (1962, 1966), Yablokov and Bel'kovich (1963), Burns (1965), Anonymous (1965), Harington (1966), Johnson et al. (1966), Krylov (1966*a*, 1968), Gol'tsev (1968), Kosygin and Sobolevskii (1971), Watson and Divoky (1972), Stirling (1974), Tomilin and Kibal'chich (1975), Pinigin and Prianish-

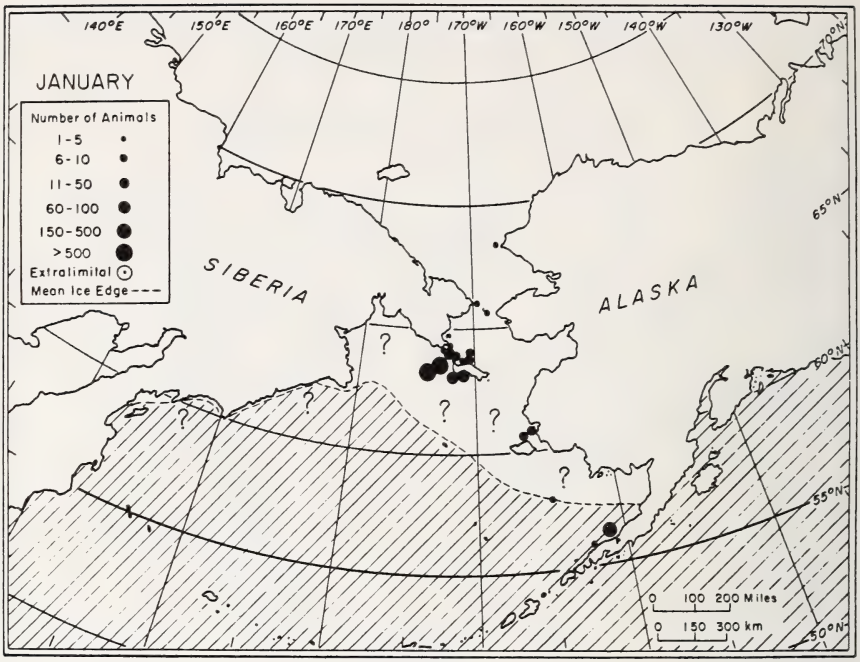

Fig. 4. Walruses sighted in January. Solid symbols indicate locations and relative numbers of animals sighted, in relation to the average position of the edge of the pack ice. Crosshatched area is open, ice-free sea. Question marks show areas that have not been surveyed in this month.

nikov (1975), Heptner et al. (1976), and Estes and Gilbert (1978). Most of the unpublished data are from aerial surveys conducted by H. W. Braham, J. J. Burns, G. A. Fedoseev, K. J. Frost, V. N. Gol'tsev, K. W. Kenyon, J. G. King, and G. C. Ray in 1960 to 1979, and from my own field notes from 1952 to 1979. Complementary information on attendant ice, weather, and oceanographic conditions was derived principally from publications by the U.S. Navy (1946, 1956, 1958), Webster (1954), Schule and Wittman (1958), Zenkevich (1963), Hood and Kelley (1974), Shapiro and Burns (1975*a*, 1975*b*), Muench and Ahlnäs (1976), and Brower et al. (1977), as well as from my field observations and interpretations of satellite imagery and those, especially, of J. J. Burns and L. H. Shapiro.

Monthly Records

January (Fig. 4)

During January, more than 90% of the sea north of Bering Strait is covered by relatively stable, heavy ice. As leads appear, they are rapidly obliterated by new ice and snow. South of the Strait, prevailing northeasterly winds tend to pack the ice tightly against the northern coast of St. Lawrence Island. The same winds tend to push the ice away from the southern coast of the island and from the southern parts of the Chukchi and Seward peninsulas. Thus, the leeward areas very often have open water or thin ice, whereas the windward sides usually have densely packed ice with few or no openings. To the east of St. Lawrence Island, the ice is mostly very heavy and closely packed; to the west, it tends to be much lighter and more open throughout the winter.

Few records of walrus sightings exist for January. That most of those are from the vicinity of St. Lawrence Island does not necessarily imply that the center of the population is there at that time. Up to this writing, there have been no surveys conducted to determine distribution of walruses in January; nearly all of the sightings indicated in Fig. 4 were recorded by observers on shore.

In most years, walruses migrating southward through Bering Strait reach or pass the latitude of St. Lawrence Island in December, slightly in advance of local development of heavy ice. During six aerial transects in January 1957 to 1968, between Nome and St. Lawrence Island, I saw no walruses north of 64°N latitude or east of 170°30′W longitude. Belopol'skii (1939) remarked that walruses were absent from the northwestern Chukchi Sea at that time, but that a few occasionally were taken by the local Chukchi and Eskimos in Bering Strait. The Eskimos on Little Diomede Island in Bering Strait also have taken a few walruses in this month in recent years but always have reported very small numbers (<10) of animals present (J. J. Burns, A. C. Heinrich, K. W. Kenyon, personal communication). Solitary animals occasionally overwinter in the Chukchi Sea, near the village of Point Hope (J. J. Burns, personal communication), and in the eastern Beaufort Sea, near Banks Island (Stirling 1974). Far to the southeast, there have been reports of a few animals in the vicinity of Nunivak and Nelson islands (R. L. Rausch, R. Tremaine, personal communication) and in outer Bristol Bay (J. J. Burns, personal communication). The largest group was about 200 that remained in the vicinity of Port Moller for 2 months in the winter of 1969 (J. E. Hemming, personal communication).

February (Fig. 5)

By mid-February, the pack ice extends southward nearly to the southern edge of the continental shelf in the western Bering Sea and to central Bristol Bay in the east. Cold, northerly winds continue to drive it southward. February is the coldest month of the year in the northern Bering Sea and the period of strongest surface winds. Therefore, it is the time of maximal ice generation and highest rate of southward movement of the pack.

The number of walrus sightings in this month is substantially greater than in January, but still inadequate to provide a detailed view of overall distribution of the population. Nearly all of the sightings at sea were recorded during aerial and shipboard surveys in the last half of the month. These sightings suggest that in most years, most of the animals are west and south of St. Lawrence Island, distributed much as indicated for March (Fig. 6); the remainder is mainly in or near Bristol Bay.

I saw no walruses north of 64°N or east of 170°40′W in two aerial transects between Nome and St. Lawrence Island. All of the animals that were sighted on those transects were close to the northwestern part of the island. Eskimos at Gambell reported that walruses were abundant in the thinner, more open ice to

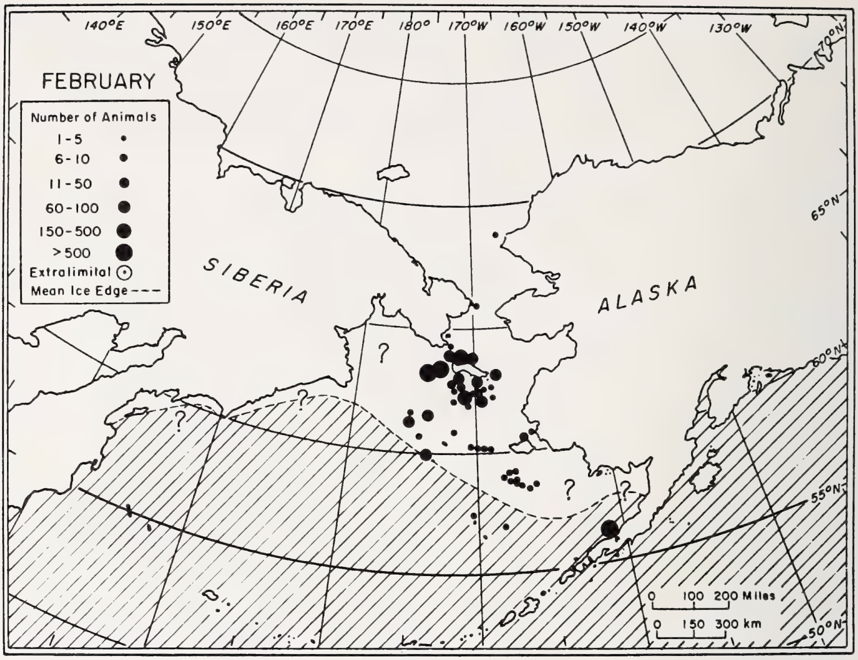

Fig. 5. Walruses sighted in February (symbols as in Fig. 4).

the west and south of the island. Occasionally, some also remained along the northeastern side of the island throughout the winter. The northernmost records in this month are of a few animals near East Cape, Chukotka (Belopol'skii 1939) and off Cape Lisburne, Alaska, in the Chukchi Sea (J. Lentfer, personal communication). The southernmost records are at Port Moller, Alaska Peninsula, and near the Pribilof Islands (J. J. Burns, J. E. Hemming, R. A. Ryder, personal communication).

March (Fig. 6)

The pack ice ordinarily attains its maximum extent in the eastern Bering Sea in March; in the west, the maximum is reached in April. Surface winds diminish somewhat during this period, and air temperatures moderate slightly; however, winter conditions still prevail.

As a result mainly of two extensive aerial surveys in 1960 and 1961 (K. W. Kenyon 1960*a* and personal communication) and two less extensive shipboard surveys in 1972 and 1976 (F. H. Fay, unpublished data), the number of walrus sightings in March is substantially greater than for the previous two months and probably reflects the winter distribution reasonably well. In general, the population appears to be divided into two major concentrations, widely separated by areas in which few or no animals were sighted. The largest of the concentrations is to the west and south of St. Lawrence Island; the smaller is in northern Bristol and Kuskokwim bays and near the Pribilof Islands.

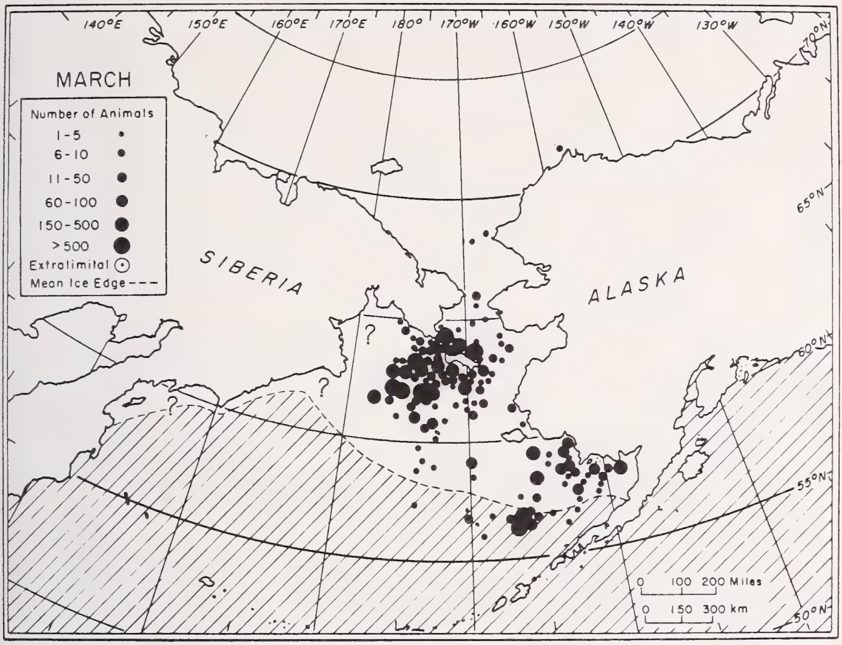

Fig. 6. Walruses sighted in March (symbols as in Fig. 4).

Conceivably, a third, smaller group exists along the Koryak coast, southwest of Cape Navarin (cf. Fig. 7), but no data are available from that sector in March.

The distribution at this time probably is much the same as it is in February, but there are suggestions of some initial movement northward, especially in the vicinity of St. Lawrence Island and Bering Strait. The first sightings north of 64°N and east of 170°40'W were recorded in March, though in only 4 of 17 winters between 1956 and 1972. Large numbers also were sighted there in March 1976 (H. W. Braham, personal communication). In some years, an increase in numbers from February to March also was seen in the vicinity of Bering Strait, near and to the north of the Diomede Islands. The most northerly sightings were of two animals near Barrow, Alaska (H. Melchior, personal communication), and of a few males just west of Point Hope (Manville 1961; S. J. Harbo, personal communication). The southernmost sightings were near the Pribilof Islands (F. H. Fay, K. W. Kenyon, unpublished data). At this time also, a few individuals have been seen near shore along the southern coast of Chukotka (Belopol'skii 1939; Nikulin 1941) and off the Alaskan coast near Hazen Bay and Tununak (K. W. Kenyon, R. Tremaine, personal communication).

April (Fig. 7)

With the increasing angle and duration of solar radiation and lighter, more variable winds, the weather over the Bering Sea is appreciably warmer in April than in the previous months, and the rate of formation of new ice is diminished.

At the same time, rising water temperatures in southeastern Bering Sea lead to more rapid melting of ice at the southern border of the pack and the beginning of general recession northward. To the north, there is loosening of the pack in all areas.

Dispersion of walruses from their areas of winter concentration is abundantly evident throughout the pack ice in April. Those animals that winter in the Bristol–Kuskokwim Bay area begin to move northward along the Alaskan coast; apparently those in the Pribilof area begin their migration northwestward toward the Gulf of Anadyr. The major concentration of animals to the south and west of St. Lawrence Island disperses more into the Gulf of Anadyr, and especially northeastward toward Bering Strait.

A small, third concentration in the western Bering Sea, east of Cape Navarin, was indicated by Kenyon's (1972) data. Probably, this group overwintered along the Koryak coast, southwest of Cape Navarin, and was bound for northwestern Anadyr. A similar concentration was sighted in this same area in April 1979, and other small groups, including females with calves, were present on the Koryak coast (G. A. Fedoseev, personal communication). Judging from the general tendency for northward movement in April, I presume the Koryak animals move northward to Kresta Bay.

To the north, the first walruses appear in Kresta Bay, and large numbers are present in Bering Strait. A few have been sighted at the latitude of Point Hope (S. J. Harbo, J. Swiss, personal communication) and rarely near Barrow (J. J. Burns, personal communication). A single male sighted near the northwestern corner of Banks Island in early April (Stirling 1974) certainly was one that had overwintered there, rather than having been part of the vanguard of northward migrants. Distributional extremes in the southern Bering Sea include a herd sighted in Korf Bay, northern Karagin Gulf in 1968 (Kosygin and Sobolevskii 1971), and large herds (about 100 each) sighted on Amak Island near the southwestern end of the Alaska Peninsula in 1962 and 1969 (K. W. Kenyon, K. B. Schneider, personal communication). In addition, there have been at least three extralimital records for April from the North Pacific Ocean: an adult female in Uyak Bay, Kodiak Island, in 1954 (R. A. Ryder, personal communication), a subadult female in the Knik River, near Anchorage in 1964 (F. H. Fay, unpublished data), and a herd on Egg Island, Shumagin Islands, in 1979 (C. A. Smith, personal communication).

May (Fig. 8)

By late April or early May of most years, formation of new ice ceases in the Bering Sea, and melting of the submerged parts of the floes becomes evident not long thereafter, even in Bering Strait. At the same time, surface winds become much weaker and more variable in direction, which usually leads to cessation of the general north-to-south trend of ice movement. By the end of May, the ice that had covered nearly the entire shelf of the Bering Sea for the previous 4 months is reduced to a few large, wind-rafted masses of heavy floes that generally cover less than one-fourth of that area. Meanwhile, in the Chukchi Sea, a major flaw opens widely along the northwestern coast of Alaska, and there is increasing occurrence of open leads and polynyas in the area between Point Hope and Bering Strait.

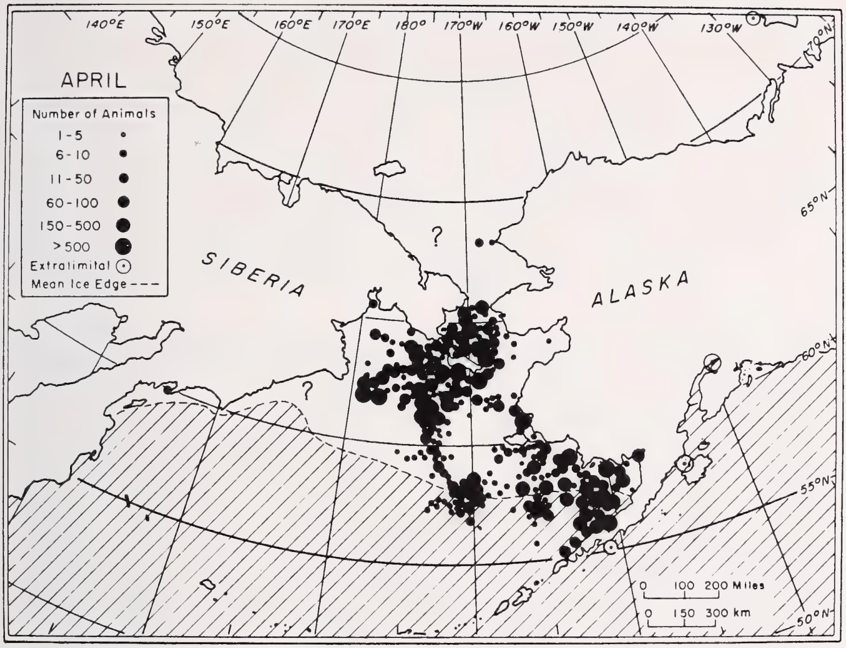

Fig. 7. Walruses sighted in April (symbols as in Fig. 4).

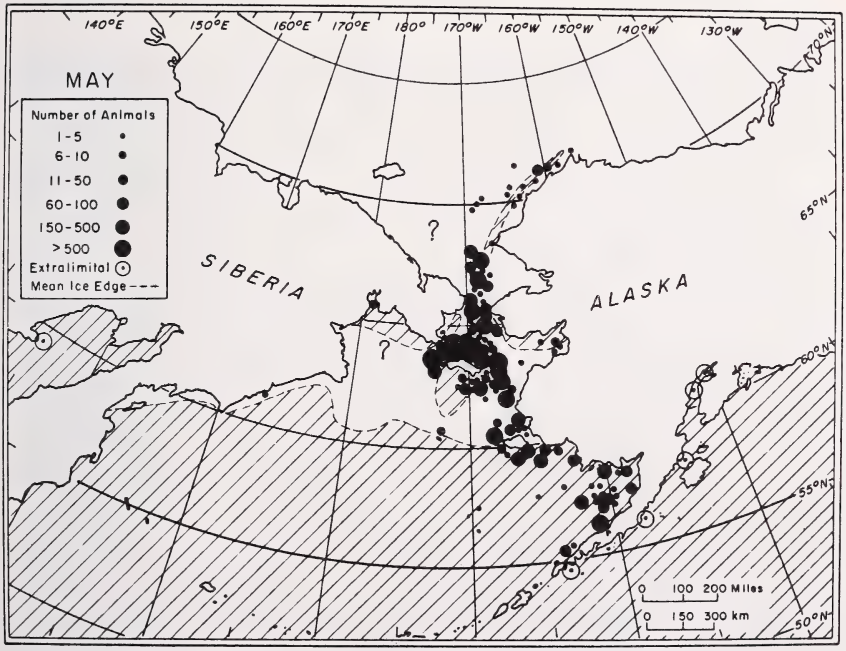

Fig. 8. Walruses sighted in May (symbols as in Fig. 4).

A large part of the walrus population passes northward through Bering Strait in May, and in some years the vanguard may advance as far as Barrow. Apparently, the bulk of the population still is situated between St. Lawrence Island and Bering Strait, although the scarcity of data from the Gulf of Anadyr and from the Chukchi Sea west of 170°W precludes documentation of movements into those areas. Probably there are large numbers in the northern Gulf of Anadyr (cf. Fig. 9), but they may be widely dispersed, for only small groups have been sighted west of 175°W (G. A. Fedoseev, personal communication). Because the ice north of Bering Strait is considerably more compact in the west than in the east, migrants probably are scarce in the southwestern Chukchi Sea at this time.

The northernmost records near Barrow were obtained during a transit to that area from the south by the icebreaker *Northwind* in 1954 (R. A. Ryder, personal communication). The southern maxima in the Bering Sea include groups sighted on the Koryak coast in 1964 and 1979 (Kosygin and Sobolevskii 1971; G. A. Fedoseev, personal communication) and at Cape Glazenap and Unimak Island, near the southwestern end of the Alaska Peninsula (K. W. Kenyon and C. A. Smith, personal communication). Extralimital records, outside the Bering Sea, were of a young female on the Yamsk Islands in the northeastern Okhotsk Sea in 1940 (Moiseev 1951 *in* Heptner et al. 1976), one in False Pass in 1979 (R. Tremaine, personal communication), three in Chignik Lagoon in 1979, one in Shelikof Strait, west of Kodiak Island in 1979 (C. A. Smith, personal communication), and single animals in upper Cook Inlet in 1955 and 1979 (L. Temple and K. W. Pitcher, personal communication).

June (Fig. 9)

The rafted remnants of the winter pack in the Bering Sea continue to diminish through melting, and by the end of June little ice remains except in the Gulf of Anadyr and just east of St. Lawrence Island. However, north of Bering Strait, in the Chukchi Sea, the pack remains more or less intact. In addition to the broad flaw along the northwestern Alaskan coast, another begins to open along the northern coast of Chukotka, providing an avenue for dispersal of walruses toward Wrangell Island.

In June, most of the remainder of the population moves northward through Bering Strait, mainly along the rafted ice that extends to that area from the eastern end of St. Lawrence Island. At the same time, the vanguard in the western Chukchi Sea has dispersed to the vicinity of Long Strait and Wrangell Island. Unfortunately, there are no data to indicate the pattern of that dispersal. Several thousand animals, principally males, appear at this time also in the northern Gulf of Anadyr and in Bristol Bay, where they will remain for the summer. In some years, large groups have been sighted also along the Koryak coast, from Cape Navarin to Karagin Gulf, and along the Alaskan coast from Kuskokwim Bay to Norton Sound.

The northernmost records in this month are of individuals on the southern coast of Banks Island, Northwest Territories (Harington 1966) and near the northwestern coast of Wrangell Island (Nikulin 1941). The southernmost records in the Bering Sea are from the Commander Islands (Chugunkov 1970 *in* Kosygin and Sobolevskii 1971) and Amak Island (J. Sarvis, personal communication).

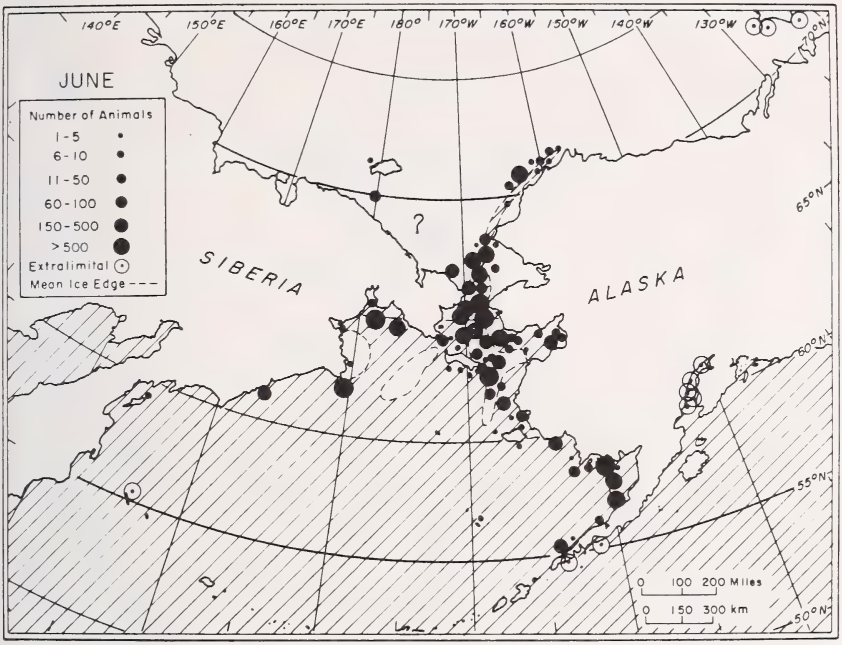

Fig. 9. Walruses sighted in June (symbols as in Fig. 4).

Extralimital records include sightings at False Pass, Wosnesenskii Island, and in Cook Inlet in 1979 (C. A. Smith, R. Tremaine, K. W. Pitcher, personal communication).

July (Fig. 10)

The last remnant of the Bering Sea pack persists in the southwestern Gulf of Anadyr usually until the end of this month. To the north in the Chukchi Sea, the edge of the main pack usually recedes to about 70°N by that time. Meanwhile, ice in the eastern Beaufort Sea also has begun to open up. Walruses are abundant off the northern coast of Chukotka from Bering Strait at least as far west as Long Strait, while in the eastern Chukchi Sea, large groups are situated between Icy Cape and Barrow. South of Bering Strait, the animals found along both the Alaskan and Siberian coasts are mainly those that will remain there during the summer. These use the Arakamchechen, Rudder, and Meechken hauling grounds on the Siberian coast and Round Island in northern Bristol Bay. Practically all of these animals are males.

The most northerly records at this time are at Predatel'skii Bay, Wrangell Island (Tomilin and Kibal'chich 1975), at 72°N, 165°W (H. W. Braham, personal communication) and at Holman Island, Northwest Territories (Harington 1966). To the south, several animals have been sighted along the Koryak coast at Natalia Bay (Nikulin 1941) and at Bogoslov Island, Cape Zosimy, and Lavrov Bay (Kosygin and Sobolevskii 1971); others have been seen

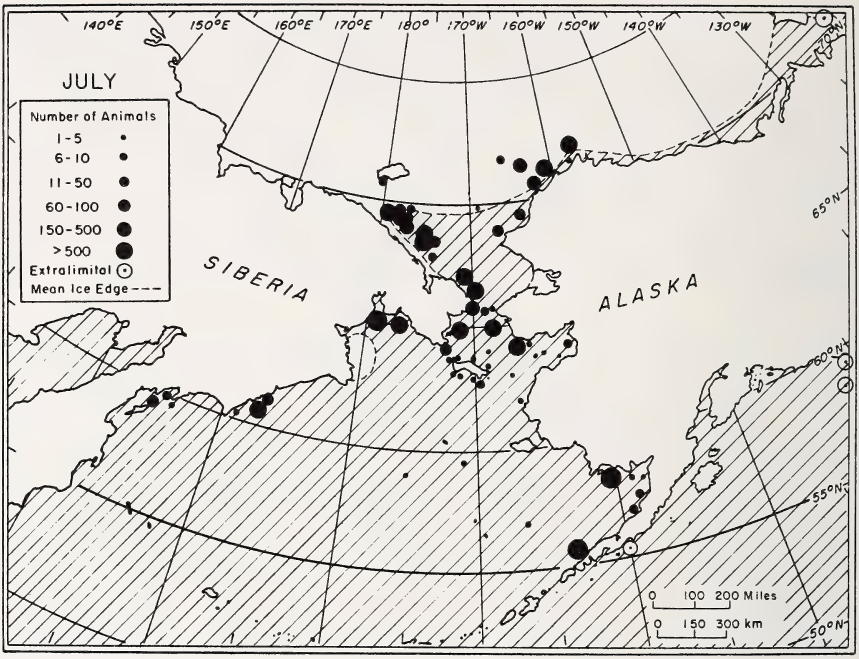

Fig. 10. Walruses sighted in July (symbols as in Fig. 4).

in northern Karagin Gulf at Cape Paklan and Korf Bay (Nikulin 1941) and on Verkhoturov Island (Heptner et al. 1976). In the eastern Bering Sea, the southernmost records for this month were at Amak Island (J. Sarvis, personal communication), and east of the Pribilof Islands (R. A. Ryder, personal communication). Extralimital records were from the vicinity of Yakutat Bay in 1979 (D. G. Calkins, H. W. Braham, personal communication).

August (Fig. 11)

During August, the edge of the pack ice generally retreats northward to about 71°N in the Chukchi and Beaufort seas and to a lesser extent in the East Siberian Sea. At this time most of the walrus population disperses northwestward to the vicinity of Wrangell Island. Many animals also remain along the northern coast of Chukotka and off the northwestern coast of Alaska, between Icy Cape and Barrow.

The extremes of distribution in the northwest in August have been near the Bear Islands in the East Siberian Sea and at 74°22′N, 165°W in the Arctic Ocean (Anonymous 1965); in the northeast they have been near Herschel Island, Yukon Territory and the Baillie Islands, Northwest Territories, in the Beaufort Sea (Harington 1966). Southernmost records have been at Verkhoturov Island in Karagin Bay (Nikulin 1941) and at Amak and the Pribilof Islands (Wilke 1942; J. Sarvis, personal communication).

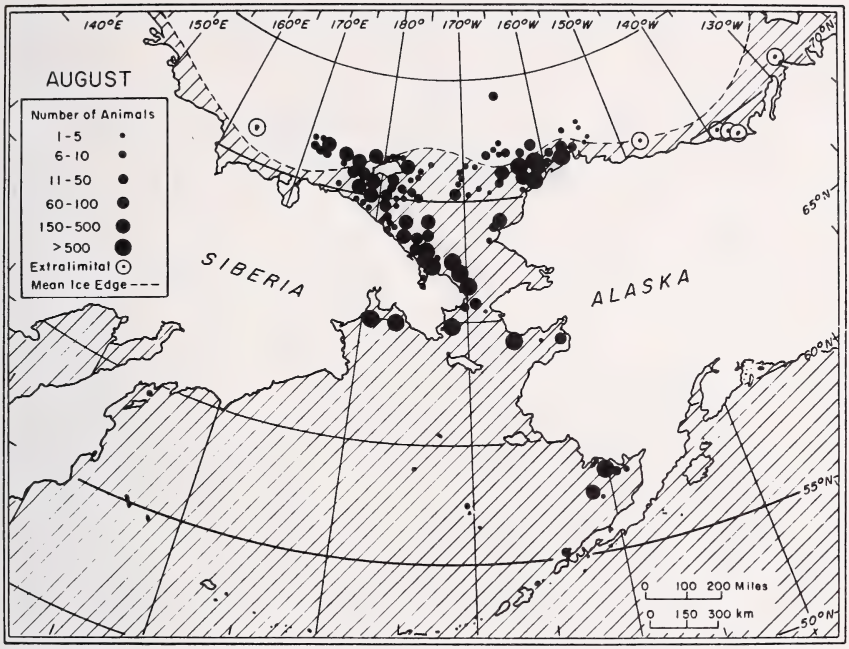

Fig. 11. Walruses sighted in August (symbols as in Fig. 4).

September (Fig. 12)

The pack ice usually retreats to its least extent in September, and the mean position of its southern edge at that time in the central Chukchi Sea is about 74°N. To the east and west, the edge is substantially farther south, and there is some formation of new ice, especially in the East Siberian and Beaufort seas.

Apparently, most of the walrus population at this time is situated north of 70°N. In years when the ice retreats far to the north, the animals haul out on Wrangell Island in enormous numbers, particularly at Cape Blossom (Gol'tsev 1968; Tomilin and Kibal'chich 1975). A large number of animals remains along the northern coast of Chukotka and in the vicinity of Barrow. Other herds are distributed along the fringe of the pack between Barrow and Wrangell Island but are concentrated mainly east of 170°W and west of Herald Island (Estes and Gilbert 1978; J. J. Burns, personal communication). To the south, large herds of males remain on Big Diomede (Ratmanov) Island and on the Arakamchechen, Rudder, Meechken, and Round Island hauling grounds. In some years, individual migrants first appear in late September at St. Lawrence Island and on the coast of western Alaska between the Kuskokwim and Yukon deltas.

The western, northern, and eastern limits of distribution in the northern part of the range in September have been established respectively, by sightings at 70°24'N, 166°55'E and near Cape Shelagskii in the East Siberian Sea (Anonymous 1965), at 75°35'N, 179°58'W and at 75°52'N, 164°15'W in the Arctic Ocean (Krylov 1968; C. A. Barnes, personal communication), and at

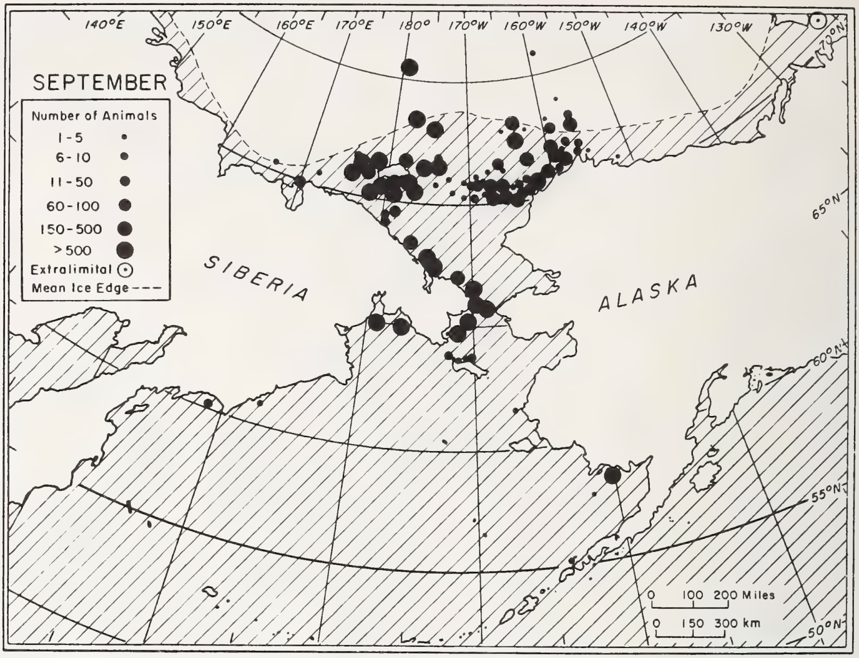

Fig. 12. Walruses sighted in September (symbols as in Fig. 4).

Holman Island, Northwest Territories (Harington 1966). To the south on the Siberian coast, walruses have been sighted on Bogoslov Island and in Olyutorskii Bay in the Koryak region (V. N. Gol'tsev, personal communication), and in Listvenichnoi and Russkoi bays, Kamchatka (Chugunkov 1970 *in* Kosygin and Sobolevskii 1971). The southernmost sightings in Alaska were at Amak Island in 1979 (J. Sarvis, personal communication).

October (Fig. 13)

With abundant formation of new ice, the pack rapidly advances southward in October, and its southern edge frequently is below 70°N by the end of that month. At the same time, the walruses also advance southward, mainly ahead of the ice, and to judge from the distribution of sightings in this and the previous month, possibly in two or three "waves." Apparently, the first to arrive in Bering Strait are those that have summered along the northern coast of Chukotka. Those summering in the Barrow and Wrangell Island regions appear to remain there somewhat longer.

Enormous herds of southbound migrants congregate on the hauling grounds in Bering Strait and on the Punuk Islands, just east of St. Lawrence Island. At the same time, large numbers have appeared in the vicinity of Nunivak and Nelson islands, on the Alaskan coast, presumably having swum there from the north. The herds that have summered in the northern part of the Gulf of Anadyr desert the Meechken and Rudder hauling grounds usually in late September, but a large

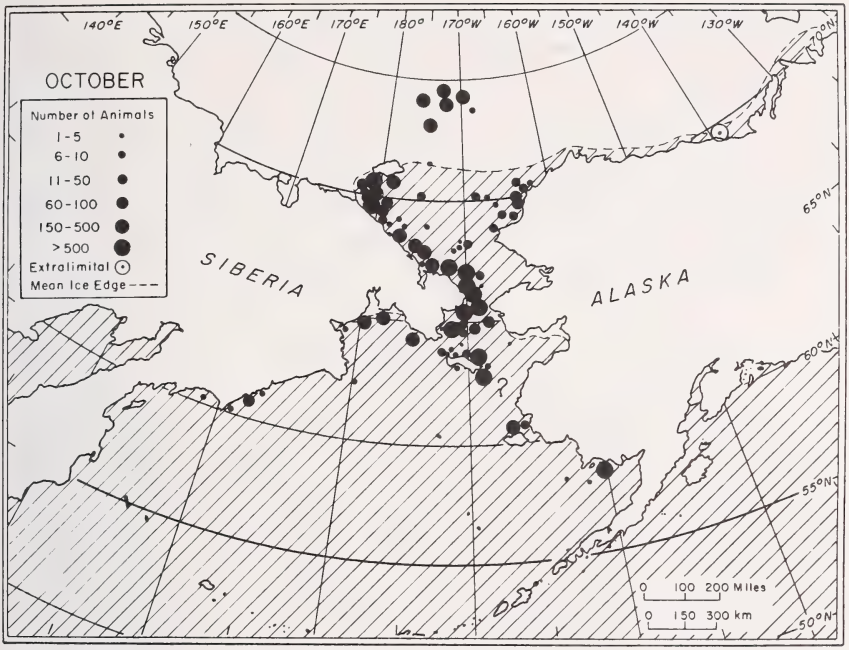

Fig. 13. Walruses sighted in October (symbols as in Fig. 4).

number of animals continues to use Round Island in Bristol Bay throughout October.

The extremes of range in the north in this month are about 178°E, in Long Strait (Anonymous 1965), about 74°40′N, 173°20′W (R. V. Miller, personal communication), and Herschel Island, Northwest Territories (Porsild 1945). In the south, on the Siberian coast, there have been sightings about 60 km east of Cape Navarin, off Anastasia Bay, at Bogoslov Island, near Cape Vitgenshtein, and in Olyutorskii Bay (V. N. Gol'tsev, personal communication). On the Alaskan side, no sightings have been reported south of northern Bristol Bay (J. Clarke, H. W. Braham, personal communication).

November (Fig. 14)

The mean edge of the pack ice in November is in or just south of Bering Strait, and most of the walrus population probably is concentrated between it and St. Lawrence Island for much of the month. Unfortunately, there are few data for November on which to base judgment. For most of the month, large herds of several thousand animals remain on and near Big Diomede, Arakamchechen, St. Lawrence, and the Punuk islands, but I have no sightings from the Soviet area south of Arakamchechen and very few from the Alaskan side south of St. Lawrence Island. The Meechken and Rudder hauling grounds in northern Gulf of Anadyr are not occupied in November, although the Round Island hauling ground in northern Bristol Bay continues to be used (J. Faro, personal communication).

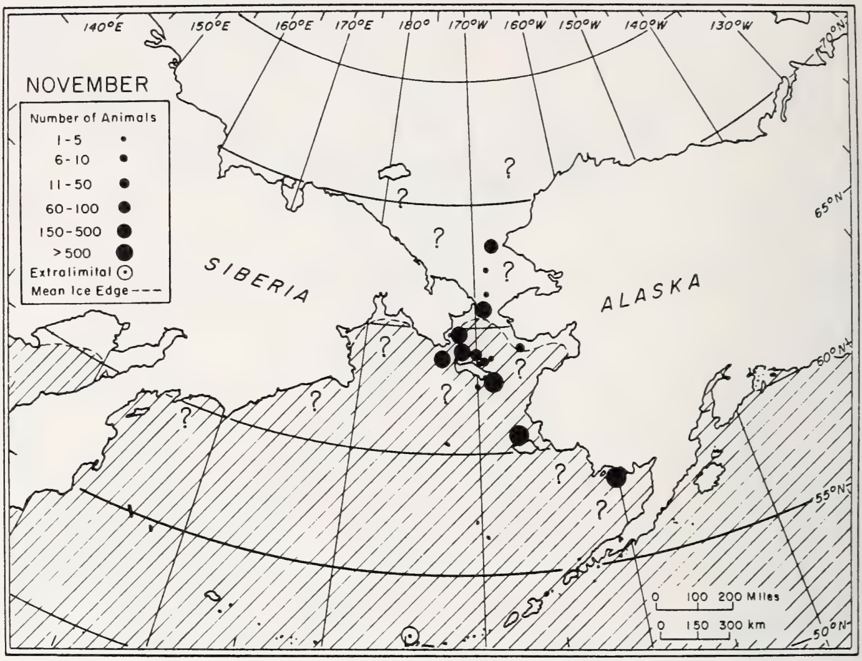

Fig. 14. Walruses sighted in November (symbols as in Fig. 4).

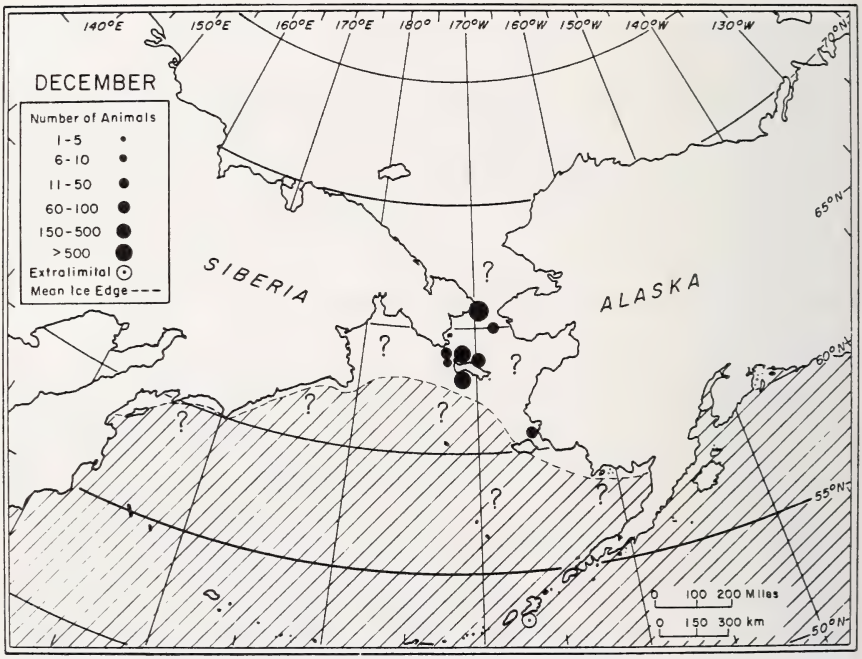

Fig. 15. Walruses sighted in December (symbols as in Fig. 4).

The southernmost record in the Bering Sea is of a single male taken at Atka, in the central Aleutian Islands in 1972 (K. W. Kenyon, personal communication).

December (Fig. 15)

The northern part of the Bering Sea, south to about 63°N, becomes covered by new ice usually in mid- to late December. Before that ice develops, large herds of walruses are present in Bering Strait and in the vicinity of St. Lawrence Island. Apart from one sighting near Unalaska Island in 1976 (C. A. Smith, personal communication), there are no data concerning distribution or movements elsewhere in or near the southern Bering Sea at that time.

Environmental Factors

A close correlation between the distribution of the Pacific walrus population and the extent and character of the pack ice is apparent from the foregoing summary. Throughout the year, these animals occur mostly in or near the southern periphery of the pack or in other areas within the pack where open leads and thin ice are continually present. They are not generally found where heavy, snow-covered ice occupies more than 80% of the sea's surface. Where much of the cover is young, gray ice, the animals' movements are almost unrestricted, for they are able to create breathing holes at will by breaking up through ice up to 20 cm thick (Fig. 16). Although they can maintain holes in heavy, snow-covered ice, they seem to avoid areas where this is necessary, such as in the Chukchi Sea in winter, the southern Gulf of Anadyr, and areas north and east of St. Lawrence Island.

As Brooks (1954) observed, their migrations through Bering Strait in spring seem to coincide with the most favorable ice movements. Southerly winds and sea surface currents cause the ice to drift northward through the Strait much of the time in May and June, and any walrus that rests on it is transported toward the north without the slightest effort. Strong winds from the north and east also are not uncommon in spring in the northern Bering Sea, and by their force the ice often is moved in the "wrong" direction for several days or weeks at a time. Since ice seems to be used as a resting place, irrespective of the direction in which it is moving, this southerly drift often works to the disadvantage of the migrants. The principal progress in migration, however, is achieved by swimming. A walrus swimming at its normal speed of about 10 km/h could easily complete the journey from Bristol Bay to Wrangell Island (about 1,800 km) in 7 to 8 days, if it did not stop to rest. However, these animals seem not to progress with such purpose but to travel at a more leisurely rate, feeding and swimming for a time, then resting on the ice nearby. My impression from field observations is that they swim most purposively during stormy periods and when passing through areas where there is no ice on which to rest.

Conditions during the southward migration in autumn ordinarily are much different from those in the spring. Although persistent northerly winds blow the ice in the "right" direction much of the time, most of that ice is too thin to support resting walrus herds, and they usually swim ahead of it in the open sea. On arriving in the vicinity of a traditional hauling ground, they go ashore to rest, or they support themselves with their tusks along the edge of the shorefast ice.

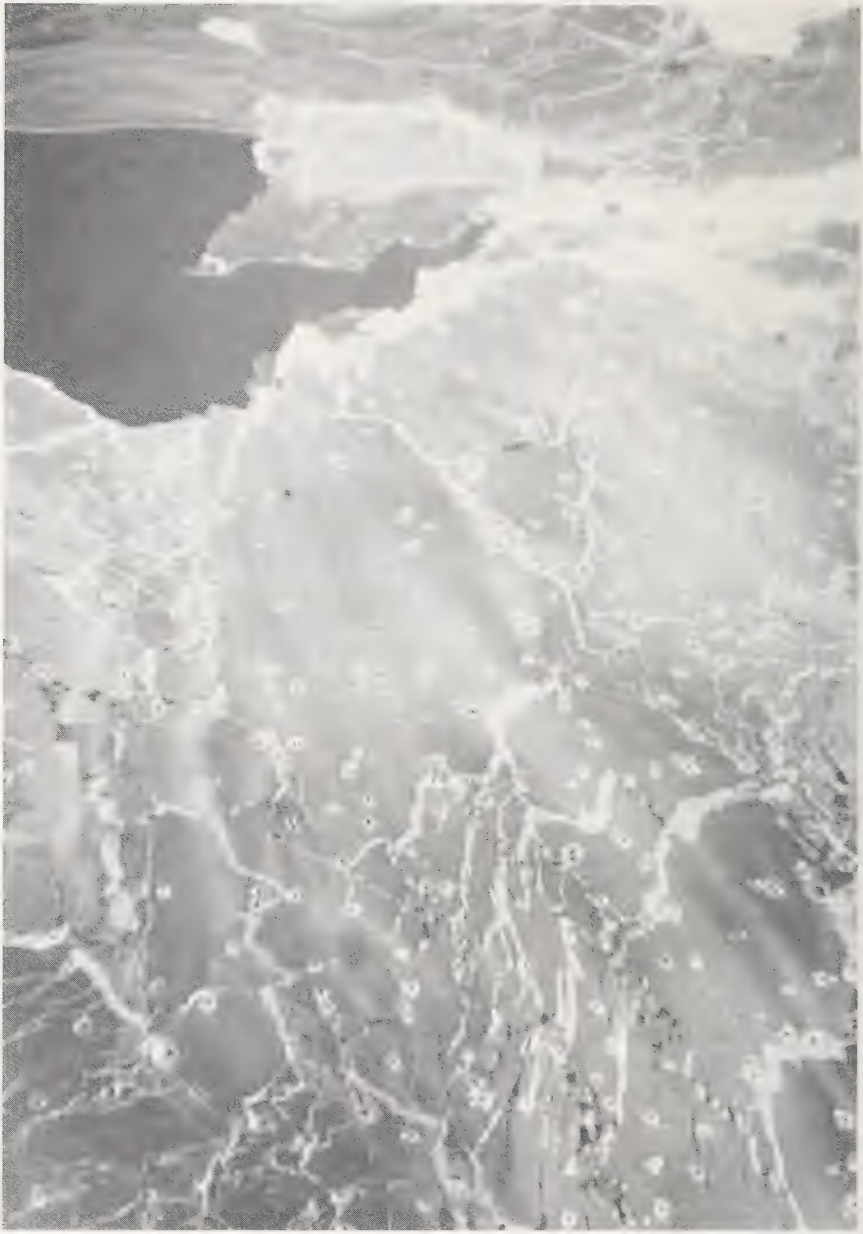

Fig. 16. Aerial view of holes made by walruses in ice about 15 cm thick. The elliptical shape is characteristic, as is the opaque area around each hole. Dark area at upper left is open water. (Photo by F. H. Fay)

Their progress is somewhat more rapid in autumn than in the spring migration, presumably due to the greater proportion of time spent in swimming toward their goal.

Adult females with dependent young are the most strongly migratory, judging from their near absence from the Bering Sea in summer. That adult males are least migratory is indicated by their occurrence in large numbers at traditional all-male hauling grounds on Rudder, Meechken, Arakamchechen, Big Diomede, and Round islands (and formerly, on the Pribilof Islands) throughout the summer. Female northern fur seals (*Callorhinus ursinus*) also are more strongly migratory than males (Kenyon and Wilke 1953), and this is true also of many species of birds. Dorst (1961) suggested that the migration of males may be inhibited by gonadal recrudescence following the breeding season. Certainly, recrudescent changes in the testes are well under way in most adult male walruses at the time of the spring migration, whereas many of the subadults and juveniles are in the peak of their rut at that time. There are indications that the migratory males are predominantly of those younger age classes; most of the males that remain in the Bering Sea in summer are the older adults (Fedoseev and Gol'tsev 1969).

Subadults of either sex seem most inclined to wander or to be diverted by irregular ice movements. Extralimital strays and animals sighted in the periphery of the Bering–Chukchi region are most often subadults or young adults. Since 1930, the limits of wandering in the south have been Honshu, Japan (Scheffer 1958), northeastern Okhotsk Sea (Moiseev 1951 *in* Heptner et al. 1976), Atka Island in the Aleutian Chain (K. W. Kenyon, personal communication), and Yakutat Bay in the Gulf of Alaska (D. G. Calkins, personal communication). In the north, the limits have been the Bear Islands, East Siberian Sea (Chapskii 1940), 75°52'N, 164°15'W in the central Chukchi Sea (C. A. Barnes, personal communication), and Bathurst Inlet, Canada (Harington 1966).

The distribution appears to be limited by bathymetry (Fig. 17). The animals ordinarily do not occur in areas where the water is more than 80 to 100 m deep, presumably because they cannot feed efficiently or are not capable of diving in greater depths (Vibe 1950). I have observed walruses feeding in the Bering Sea in areas that ranged in depth from 25 to 79 m.

In winter, the distribution appears to be influenced also by ice conditions, as noted earlier. Comparison of the distribution of walruses in March (Fig. 6) with that of the pack ice (Fig. 18) indicates that the animals tend to concentrate in areas where the ice is darkest (thinnest or most dispersed) and to be scarce or absent from the areas where it is whitest (heaviest and most compact). The ice pattern indicated in Fig. 18 is about average for February and March. Although the southward extent of the ice varies widely from year to year in the eastern Bering Sea, the overall pattern of light and heavy ice prevails in most years (Brower et al. 1977; J. J. Burns, L. H. Shapiro, and F. H. Fay, unpublished data). An exception to this may have occurred in 1967, when the southern edge of the pack in mid-April was in the vicinity of St. Lawrence Island and Norton Sound. At that time, most of the walrus population was in the St. Lawrence Island to Bering Strait region (J. J. Burns, personal communication).

The factors limiting distribution in summer are less clear, other than that the 100-m isobath and extent of the pack ice play major restrictive roles to the north.

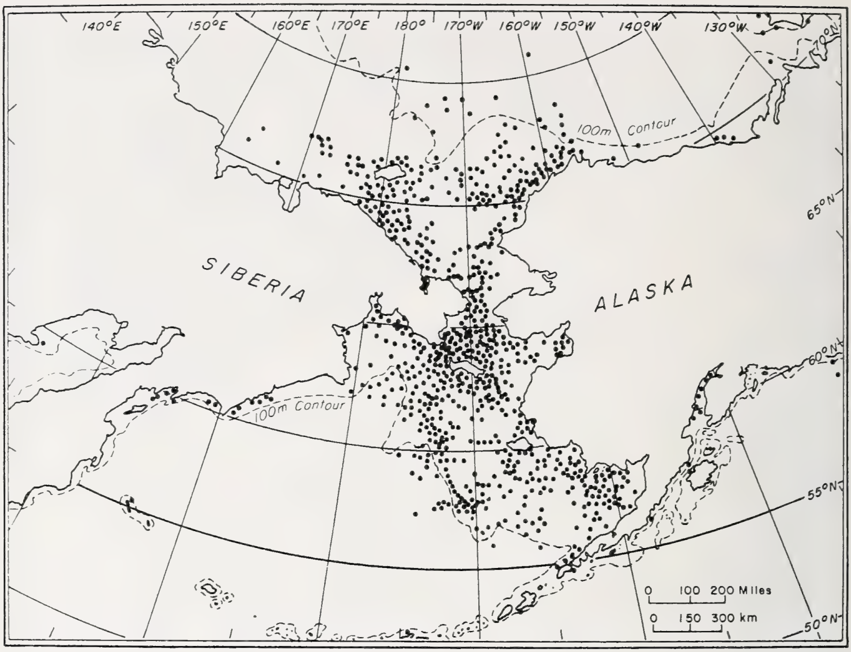

Fig. 17. Distribution of sightings of walruses (all months, 1930–79) in relation to the position of the 100-m isobath in the Bering–Chukchi region. Each dot represents one sighting, regardless of the number of animals.

Even when the eastern and western passages are open beyond Barrow and Long Strait, however, only a few animals stray outside the area bounded by 155°W and 175°E longitude (Figs. 11 and 12). The failure of more animals to move into the Beaufort and East Siberian seas in late summer is somewhat of an enigma but suggests that the conditions (food?) there are not satisfactory for walruses or, at least, are less satisfactory than those west of Barrow and near Wrangell Island.

There seem to be no physical limits to distribution of walruses south of the Bering Sea, except that the continental shelf is much narrower and the climate much warmer than to the north. Benthic invertebrates are abundant in the sublittoral and shoal waters of the North Pacific Ocean, and many of the same species of mollusks that are ordinarily eaten by walruses occur as far south as Puget Sound and Japan (MacGinitie 1959). The possibility that climate is the principal limiting factor was investigated by Fay and Ray (1968) and Ray and Fay (1968) with inconclusive results, but there were numerous suggestions of negative response to solar radiation and air temperatures exceeding those in the southern Bering Sea. During warm summer days at Round Island, the animals on the hauling grounds tend to remain at the water's edge or offshore, apparently in response to excessive heat on the beaches (Miller 1975*a*, 1976, and unpublished data).

Canadian biologists have indicated that the traditional hauling grounds in

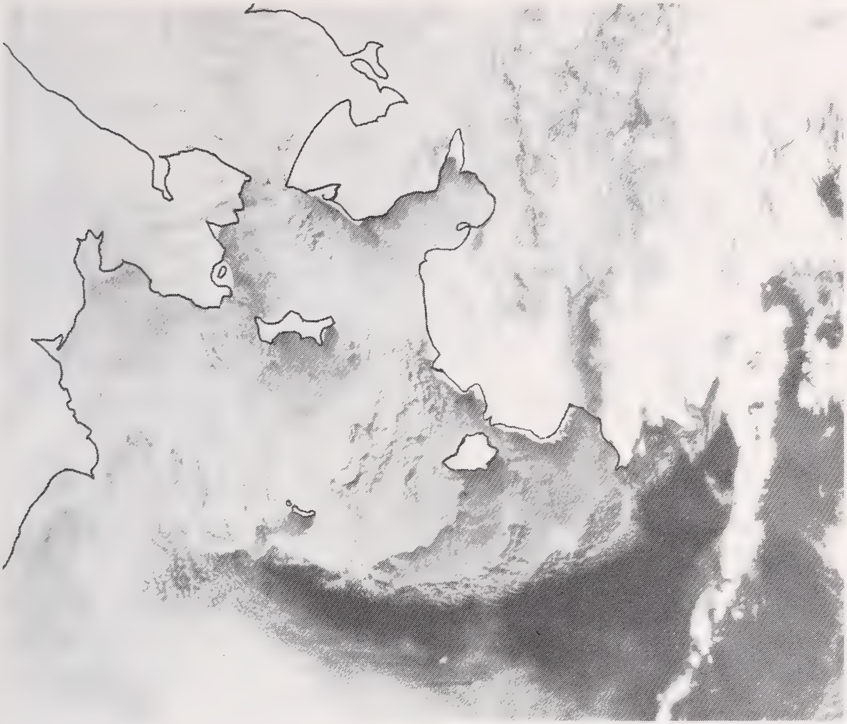

Fig. 18. Visual band image of the Bering–Chukchi region on 21 March 1978, received from the NOAA 2 Weather Satellite, showing the distribution of the seasonal pack ice. Dark areas are open water or thin ice; the whitest areas are the snow-covered continents and islands (outlined). Whitish area at lower left is low clouds.

eastern Canada consistently have low, rocky shorelines with a steep or shelving subtidal zone (Loughrey 1959; Mansfield 1959). However, the sites utilized in the Bering and Chukchi seas are more diverse, ranging from steep to gentle slopes with beach materials varying from fine sand to massive rock outcrops. Beaches adjacent to extensive shallows exposed at low tide are not used. Use of hauling grounds on shore seems to be very much influenced also by sea state and the presence or absence of floating ice. During storms with strong onshore winds and heavy surf, the hauling grounds usually are abandoned or remain unoccupied (Nikulin 1947; F. H. Fay, unpublished data). Several observers have noted that walruses confronted with the choice of ice or land for a resting place always selected the ice (Chapskii 1936; Tsalkin 1937; Nikulin 1947; Popov 1958; Loughrey 1959; Mansfield 1959).

The use of ice in preference to land conveys some considerable advantages, foremost of which, in my opinion, are nearness to the food supply and freedom from disturbance when resting (Fay 1974). These mammals, being principally predators on benthic invertebrates, probably require a rather large area in which to feed, for their prey are relatively immobile, of small size relative to the predator, and slow to reproduce. By using the moving ice, walruses are continually transported to new feeding grounds while they rest. They can find suitable hauling-out sites near almost any food source that they locate on the Bering–Chukchi shelf. By staying with the ice, they are able to exploit the benthic resources of nearly the entire shelf, rather than being limited to areas within foraging range of coastal hauling grounds.

A major advantage of ice also is its distance from terrestrial predators, especially man. This advantage was clearly demonstrated during the 18th and 19th centuries, when most of the herds that regularly frequented coastal and insular sites in the Bering and Chukchi seas were extirpated (Fay 1957). Herds that stayed with the ice survived in some numbers, probably because they were less accessible and their location less predictable. In general, the same can be said of walrus populations in other parts of the Arctic; some that resided almost entirely on coastal hauling grounds in summer are now extinct or close to extinction (Bel'kovich and Khuzin 1960; Reeves 1978).

Concentrations and Migrations

The use of ice as a means to exploit the Bering–Chukchi shelf requires most of the walruses to migrate long distances during the annual advance and retreat of the pack. In his description of those migrations, Belopol'skii (1939) theorized that the population was not unified but was made up of three separate segments, which he called the Kresta, Wrangell, and American groups. He supposed that the Kresta group separated from the main population in April–May and that it moved westward along the southern coast of Chukotka, arriving at Kresta Bay in June or July. The Kresta group was believed to retrace its route late in the summer and pass northward toward Bering Strait, where it rejoined the rest of the population. The main population was thought to divide into Wrangell and American groups somewhere along the spring migration route, one travelling to the vicinity of Wrangell and Herald islands and the other to Point Barrow and eastward to Mackenzie Bay. Both were believed to arrive at their destinations in July or August. On the return trip, in autumn, the Wrangell and American groups were believed to reunite near Bering Strait and to be joined there by the Kresta group. This concept of a tripartite summering population was upheld by Brooks (1954), who noticed two waves of migrants reaching Bering Strait in May and June and presumed that these were the Wrangell and American groups.

The data summarized in Figs. 4–15 indicate the existence usually of at least two major concentrations during the winter in the Bering Sea, one near St. Lawrence Island and the other in Bristol Bay. These concentrations have been detected repeatedly in aerial and shipboard surveys conducted in February to April 1960–61, 1968, 1972, and 1976. In each instance they were found to comprise mainly adult females with their young, together with a few adult males (Table 1). Another, smaller concentration repeatedly has been found near the Pribilof Islands. I believe that the smaller group is part of the Bristol Bay concentration, because it was not detected in February, and it seemed to move westward during March and April (Figs. 5, 6, 7). It was composed mainly of immature and subadult males (Table 1). A fourth concentration, near Cape Navarin, was discovered in April 1972 by Kenyon (1972); apparently it was not

Table 1. *Composition of samples of Pacific walruses from the St. Lawrence, Pribilof, and Bristol Bay wintering concentrations in March and April 1971–76, as determined from shipboard observations and interpretation of aerial photographs.*

				Life stage		
				Immature (both sexes)	Subadult and adult	
Wintering area and data type[a]	Month	Year	Number of animals	(%)	Males (%)	Females (%)
St. Lawrence (S)	March	1972	907	28	10	62
St. Lawrence (S)	April	1971	332	39	4	57
St. Lawrence (A)	April	1972	1171	39	3	57
Pribilof (S)	April	1971	255	2	94[b]	3
Pribilof (S)	March-April	1976	73	15	74[b]	11
Bristol Bay (A)	April	1972	621	38	6	56

[a] Data types: (A) = aerial photos; (S) = shipboard observations.
[b] More than 75% subadults; all others more than 90% adults.

sighted there in April 1976 but was present in April 1979 (G. A. Fedoseev, personal communication). Its composition has not been determined. I suspect that it is derived from a small concentration that winters southwest of Cape Navarin, along the Koryak coast.

Animals from the St. Lawrence concentration seem to be the first to reach Bering Strait in late April (Fig. 7). At the same time, those from the Pribilof and Navarin areas apparently stream northwestward toward the Gulf of Anadyr, while many of those from Bristol Bay begin to move northward along the Alaskan coast.

In May (Fig. 8), most of the St. Lawrence concentration seems to pass through Bering Strait, into the Chukchi Sea. Probably, this is the first wave of migrants that was noticed by Brooks (1954), as well as by K. W. Kenyon and J. J. Burns (personal communication), at Little Diomede Island. Apparently, some of these animals advance northeastward along the eastern Chukchi flaw, toward Barrow, while the rest make their way northwestward, toward Wrangell Island. Meanwhile, much of the Bristol Bay concentration seems to reach eastern St. Lawrence Island and Norton Sound. These animals apparently move northward through Bering Strait mainly in June as the second wave of migrants observed at Diomede by Brooks (1954) and others. Large herds also appear in June in the northern part of the Gulf of Anadyr (Fig. 9), but it is not entirely clear from whence they come. This is Belopol'skii's (1939) Kresta group, which he thought moved into that area only from the east. Probably, it also includes those that move up from the Navarin and, perhaps, Pribilof areas.

Large herds occasionally have been sighted in June near Point Hope (W. Berry, personal communication), as well as near Cape Serdtse Kamen, northeastern Chukotka, and in Long Strait (Nikulin 1941). To the south, some males from the Bristol Bay concentration remain in the vicinity of Round Island (Miller 1975*a*), and large herds have been sighted on the Koryak coast, especially in and near Anastasia Bay (Pinigin and Prianishnikov 1975; V. N. Gol'tsev, personal communication).

Nearly all of the migrants that are bound for the Chukchi Sea apparently reach that goal by the end of June. However, some movement of females and young eastward out of the Gulf of Anadyr and northward through the western part of Bering Strait continues for at least another month. This movement was recognized by Belopol'skii (1939) and has been confirmed by some of the St. Lawrence Islanders (personal communication) who formerly resided in those areas. Occasional stragglers and herds of males have appeared irregularly along the Alaskan Bering Sea coast and islands in July. Major concentrations of males have remained at Big Diomede and Arakamchechen islands, on Rudder and Meechken spits, and in Bristol Bay. Repeated sightings of herds along the southern Koryak coast and in northern Karagin Gulf (Fig. 10) suggest that some males regularly summer there, as well.

The pattern of southward migration in autumn is less clear but seems to be about the reverse of the spring migration. That is, the herds along northeastern Chukotka seem to come down through Bering Strait first, then to eastern St. Lawrence Island and to the western Alaskan coast in the Yukon–Kuskokwim region (Figs. 12 and 13), presumably heading for Bristol Bay. At the same time, those in the northern part of the Gulf of Anadyr leave the hauling grounds and probably head southward. Last to come south are those from the Barrow and Wrangell Island areas, which probably meet in Bering Strait and make their way to the St. Lawrence wintering area.

This interpretation of the migrations is unavoidably speculative, but the data indicate to me that the three summer concentrations hypothesized by Belopol'skii (1939) do exist. There are others as well along northeastern Chukotka, in Bristol Bay, and in the Koryak region. These concentrations do not appear to be discrete to the degree that he hypothesized, though the data suggest that the amount of interchange between them is not large, even in the Chukchi Sea. The Bristol Bay and Koryak summering groups appear to be entirely isolated from all others.

In years with average to heavy ice conditions, the wintering population seems to be concentrated mainly in two areas: north-central Bering Sea, to the south and west of St. Lawrence Island, and southeastern Bering Sea, from Nunivak and the Pribilof Islands to Bristol Bay. A third, smaller concentration is found in the western Bering Sea, along the Koryak coast (G. A. Fedoseev, personal communication). The amount of interchange between the two main concentrations before their northward migration is unknown but does not appear to be large. Few individuals have been sighted in the intervening area during January to March (Figs. 4, 5, 6). In most winters, the ice in that intervening area is extremely heavy and compact (Brower et al. 1977) and probably inhibits passage of walruses. In years of unusually light ice coverage, when the pack does not extend south of 61°N, this "barrier" may be absent, and division of the population into two main groups may not occur. Such light icing took place only once in the past 30 years (winter 1966–67), and walrus surveys were not conducted then until mid-April, after the ice had receded northward to 63°N and the migration was well under way (J. J. Burns, personal communication).

If my interpretations of the migrations are correct, the spring harvests at Eskimo villages along the Alaskan coast from Bristol Bay to Bering Strait, including eastern St. Lawrence Island, Nome, and King Island, may be taken in most years mainly from the animals that have wintered in Bristol Bay. Certainly the spring harvests at Gambell and eastern Chukotka are mainly from the St. Lawrence wintering concentration. At Diomede and points north, the harvests probably are of animals from both concentrations, for the distributional data suggest mixing of the two in the Chukchi Sea. Since the animals from both wintering concentrations appear to transcend international boundaries and to be cropped by both the Soviet Union and the United States, the case for bi-national research and management of the Pacific walrus population is strong.

More current, definitive distributional information clearly is needed, particularly in November to February and in May and June. Also needed is an assessment of the site fidelity of animals in the wintering concentrations and their respective representation in the apparent clumps of animals in the summering areas. This will require not only intensive distributional surveys but large-scale marking of animals in the wintering areas, as well, to trace their migrations and their relative contributions to local harvests along the migration routes. The areas in which mating and calving take place also need to be delineated. These activities can best be done on a cooperative basis by the two countries.

General Morphology and Growth

General descriptions of the major physical characters of walruses have been presented in several reports (e.g., Brooks 1954; Mansfield 1958*a*; Loughrey 1959) and will not be repeated here. However, I have investigated some of those characters in much greater detail than ever before, and because I regard the understanding of them as critically important for dispelling some myths and developing new points of view, I shall redescribe a few of them in this and the next two chapters. These include body size and weight, growth of the reproductive organs, characteristics of the skin and hair, and the development and form of the dentition. Because, in each instance, the information is related to the age of the individual, a few words on the method of age determination are necessary.

Age Determination

Before the development of modern methods of age determination for walruses, the Eskimos and other indigenous people of the North perceived that these mammals were long-lived and that their physical characteristics changed with age. To describe this, they evolved an elaborate traditional nomenclature that was useful for classifying the animals for their purposes into several broad groups by sex and relative age. Early in the present century, Soviet biologists recognized the need for greater objectivity and precision in age determination that would allow them to obtain the demographic information required for sustained-yield management of walruses. Their efforts in the North Pacific region were pioneered by Belopol'skii (1939), who observed that the tusks of these animals grow persistently at the rate of about 1 cm per year, and that the younger age classes, at least, could be recognized on the basis of the length of their tusks.

Subsequently, Chapskii (1941) and Mohr (1952) observed that thick deposits of cementum on the cheek teeth of walruses were layered in such a way that they seemed to offer promise as indicators of age. Brooks (1954) and Fay (1955) independently reached the same conclusion and established that there is a positive relation between the number of cementum layers in the teeth and the state of physical development of the individual. Investigating this relation further, Mansfield (1958*a*), Krylov (1963, 1965*a*), and Burns (1965) concluded that the number of major layers in the cementum on the cheek teeth could be used to determine precisely the age of each individual.

The validity of the foregoing conclusion has been confirmed by my findings in free-living animals and in a series of known-age animals that were reared in captivity (see Dentition). In the known-age animals, the number of completely formed cementum layers usually was equal to or slightly less than the actual age in years of the animal (Table 2). In most instances, the layers were not as clearly expressed or as regular in thickness as those in the teeth of free-living walruses, but they were comparable otherwise in structure and appearance.

All of the ages reported here were determined from counts of those annual layers of cementum, as seen in medial longitudinal sections of an incisor, lower canine, or postcanine tooth from each animal. By sectioning entire dentitions from several specimens, I determined that the number of layers is the same in each of the teeth (except the tusks) of a given individual. The number of cementum layers in the tusks usually is much lower than that in the other teeth, due to greater loss of dental tissue from abrasion.

Body Size and Weight

Length of Body

The methods for measuring body size in pinnipeds have not yet been standardized on an international basis, and unless one is acquainted with the different national standards, interpretation and comparison of measurements can be confusing and misleading. I measured lengths of dead Pacific walruses in the field in two ways:

1. Along the body surface from the anteriormost tip of the snout to the posteriormost tip of the tail flesh, with the animal lying on its back. This measurement is called "curvilinear length" by American biologists (Scheffer 1967*b*). It is similar to the "zoological length" (often designated as *Lc*) used by Soviet biologists, which is measured with the animal lying on its belly (Gromov et al. 1963). Both of these measurements are imprecise, but their use often is expedient in the field. Although I have no comparative data from animals in which both the curvilinear and the zoological length were measured, I have assumed that they are approximately equal.

2. The straight-line distance between the tip of the snout and the tip of the tail flesh, with the animal lying flat on its back and the neck extended. This is the "standard length" measurement routinely taken by American mammalogists (Scheffer 1967*b*) and is essentially the straight length of the articulated skull and axial skeleton, plus a small amount of flesh at each end. It is greater than the "horizontal length" (*Lcv*) taken by Soviet biologists, which is measured in a

straight line from nose to tail with the animal lying on its belly and the spine arched (Gromov et al. 1963).

Table 2. *Number of completely formed cementum layers in cheek teeth of some walruses of known age, reared in captivity.*

Specimen and source[a]	Sex	Age (years)	No. of layers
Moose, San Diego Zoo (LACM M1685)	M	0.3	0
Aivok, New York Aquarium (AMNH 203342)	M	0.4	0
Bosco, San Diego Zoo (BDM 477)	M	1.1	1
Hagenbeck Tierpark (ZMUH 1226)	M	1.2	0
Snowball, San Diego Zoo (LACM M1784)	F	1.2	1
Oswald, San Diego Zoo (LACM M1785)	M	1.2	1
Butch, San Diego Zoo (LACM M1786)	F	1.3	1
Seeku, New York Aquarium (AMNH 203340)	M	1.3	1
New York Aquarium (AMNH 203343)	F	1.3	1
Herbert, New York Aquarium (AMNH 164116)	M	1.9	2
Hagenbeck Tierpark (ZMUH 1587)	M	2.4	2
Ookie, New York Aquarium (AMNH 203341)	F	3.4	3
Copenhagen Zoological Garden (ZIUK 920)	F	5.2	5
Priscilla, Marineland of the Pacific	F	6.3	5
Woofy, Marineland of the Pacific	M	7.0	7
Hagenbeck Tierpark (ZMUH 3099)	F	7.1	7
Copenhagen Zoological Garden (ZIUK 748)	F	7.6	7
Raudi, Hagenbeck Tierpark (ZMUH 5925)	M	15.3	15

[a] AMNH = American Museum of Natural History, New York; BDM = "Black Douglas" Collection, National Marine Mammal Laboratory, Seattle; LACM = Los Angeles County Museum, California; ZIUK = Zoological Institute, University of Copenhagen, Denmark; ZMUH = Zoological Museum, University of Hamburg, Germany.

In 13 specimens from which I recorded both the curvilinear and the standard length, the standard length was about 93% of the curvilinear length. According to Chapskii's (1936) comparative data from about 50 specimens, the horizontal length is about 89% of the zoological length.

Most of the data on body length of walruses that are available in the literature are either curvilinear or zoological lengths. However, because American zoologists mainly use standard length for comparison of species, populations, and individuals, that measurement alone is used in this report. When only the curvilinear or zoological length of a specimen was available, I estimated the standard length as being 93% of the given length.

At birth and for at least 1 month thereafter, male and female walrus calves are about equal in length (Table 3). Many of the males already appear to be somewhat broader in the head and shoulders than most of the females, foreshadowing their eventual unequal development. In the first 2 months, the calves increase in length by about 10 to 15 cm per month. The males probably tend to grow slightly faster than the females, for that trend is clearly evident in their subsequent development (Fig. 19). In both sexes, growth in standard length is most rapid in the first 4 or 5 years and tends to approach its asymptote at 7 to 9 years. In the females, full development in length is reached at about 10 years. In the males, however, a secondary acceleration of growth takes place from about the 9th to the 13th year, and full adult length is not attained until about 15 years.

The few data available from Pacific walruses of known age that have been reared in captivity (triangular symbols, Fig. 19) indicate that their growth in length corresponded closely to that of free-living walruses. The mean length–age curves in Fig. 19 also correspond approximately to those estimated for Atlantic walruses by Mansfield (1958*a*), though they suggest that Pacific walruses are about 4 to 7% longer than their Atlantic counterparts. In both populations, the males tend to be 15 to 20% longer than the females, and the length of the newborn calves is about 35 to 40% of that of the adults.

Table 3. *Comparative standard lengths of male and female Pacific walruses.*[a]

	Standard length (cm)					
	Males			Females		
Age class	No.	Range	Mean	No.	Range	Mean
Full-term fetuses and newborn calves	6	104–122	112	11	95–123	113
Calves						
1–2 weeks	14	106–127	116	22	107–126	116
2–4 weeks	15	116–135	127	12	121–140	129
5–8 weeks	23	123–171	140	21	121–153	135
Adults: males >14 years, females >9 years	55	279–356	320	47	230–312	272

[a] Sources: Nikulin (1941), Brooks (1954), Krylov (1962), and IU. Bukhtiarov, J. J. Burns, F. H. Fay, and K. W. Kenyon (unpublished data).

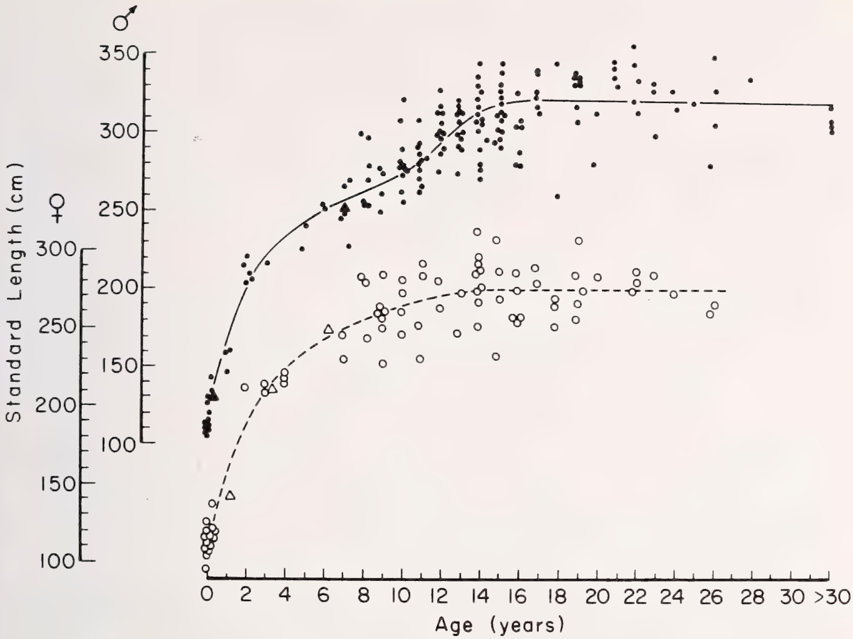

Fig. 19. Standard length of male (upper) and female (lower) Pacific walruses in relation to age. Round symbols are from animals taken at sea (J. W. Brooks, IU. A. Bukhtiarov, J. J. Burns, F. H. Fay, and K. W. Kenyon, unpublished data); triangular symbols are from animals that were reared in captivity (E. D. Asper, G. H. Pournelle, and G. C. Ray, unpublished data). Curves were fitted visually.

Weight of Body

Whole body weights of living marine mammals are difficult to obtain in the field, especially for animals as large as walruses. In this and other studies, it has been practical to obtain live weights only of very small infants. Weights of larger animals were obtained from shot specimens, almost always with some unmeasured loss of blood. In a few instances, such weights were obtained by cutting the carcass into manageable pieces, weighing each piece, and summing their weights, including those of most of the body fluids. However, in most instances, the whole carcass was weighed by hoisting it aloft with a shipboard crane, to which was affixed a suitable scale. Because of the loss of blood, the weights of most animals older than calves are conservative at best and should be regarded only as approximations of live weight.

The calves at birth and for most of the first month after birth weigh 45 to 75 kg (Table 4). By the end of their second month, they have increased in weight by only about 30%. If change in weight of captive calves is a valid guide (Fig. 20), the free-living calves probably require about 5 months to double their weight. Their weight at the end of the first year may be about three times the birth weight.

Table 4. *Comparative whole body weights of male and female Pacific walruses.*[a]

	Whole body weight (kg)					
	Males			Females		
Age class	No.	Range	Mean	No.	Range	Mean
Calves, <1 month	7	45.4– 77.1	65.1	11	46.7– 73.5	61.9
Calves, about 2 months	3	86.2– 104.3	95.3	1	95.3	–
Adults: males >14 years, females >9 years	54	880.0–1,656.0	1,210.0	34	400.0–1,250.0	832.0

[a]Sources: IU. Bukhtiarov, J. J. Burns, F. H. Fay, and K. W. Kenyon (unpublished data).

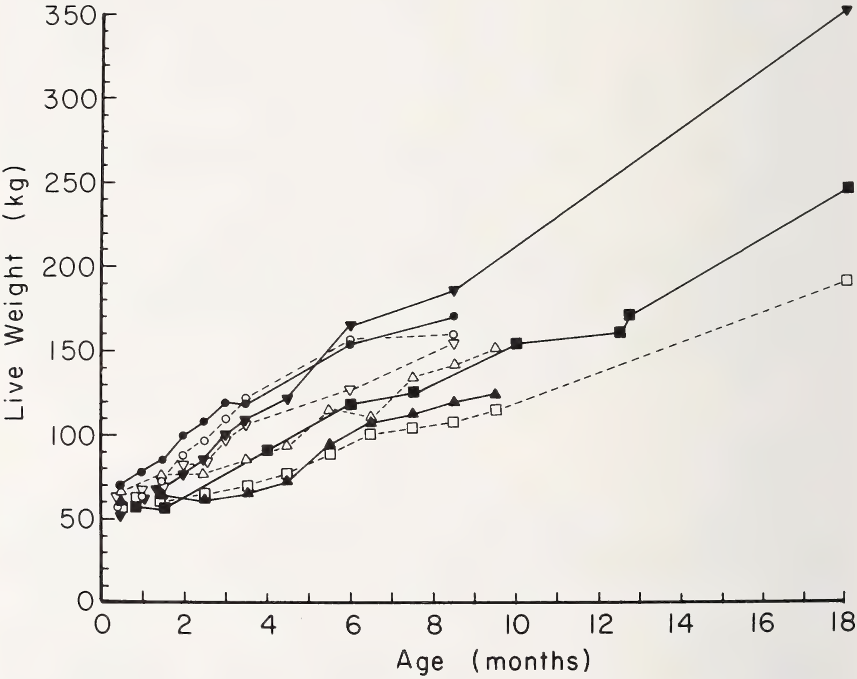

Fig. 20. Increase in weight of eight Pacific walrus calves that were reared in captivity (D. H. Brown, W. P. Heuschele, G. H. Pournelle, and G. C. Ray, unpublished data).

Growth in weight after the first year, as estimated conservatively from field weights of dead specimens and measured in a few individuals that were reared in captivity, is about as shown in Fig. 21. Females appear to reach their maximum weight (average, 830 kg) at about 12 to 14 years; males undergo a secondary acceleration in weight increase from about the 10th to the 16th year and reach their maximum weight (average, 1,200 kg) sometime thereafter. In general,

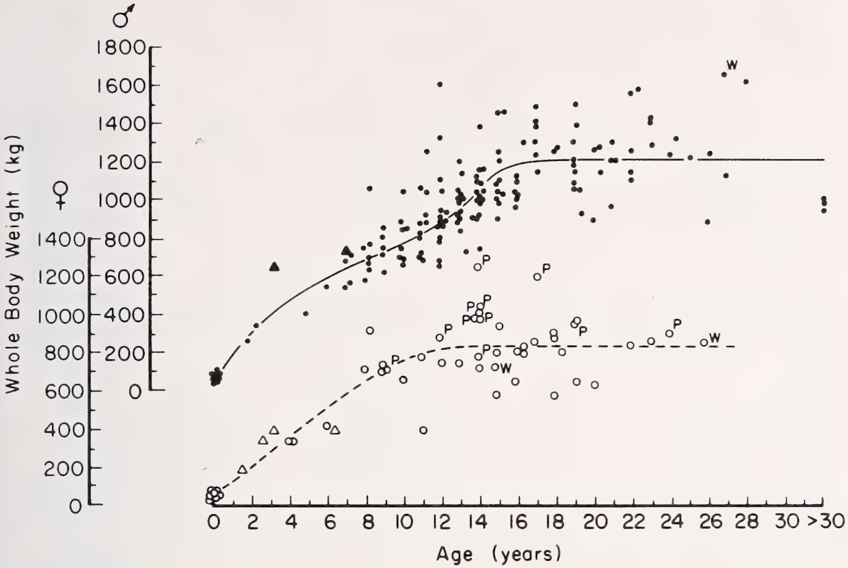

Fig. 21. Whole body weight of male (upper) and female (lower) Pacific walruses in relation to age. Round symbols are from animals taken at sea (IU. A. Bukhtiarov, J. J. Burns, F. H. Fay, and K. W. Kenyon, unpublished data); triangular symbols are from animals that were reared in captivity (E. D. Asper and G. C. Ray, unpublished data). Adjacent letters identify animals taken in winter (W) and females in or near full-term pregnancy (P). Curves were fitted visually.

adult males tend to be about 45% heavier than adult females. The weight of the calf at birth is about 8% of the mean weight of the fully developed adult female and about 5% of that of the adult male. Examples of relative weights of body parts are shown in Table 5.

Growth of Reproductive Organs

Baculum

I obtained the baculum or os penis from 273 males killed at St. Lawrence Island during the months of May and June. These were fleshed and dried in the field and later boiled in a 5% aqueous solution of sodium bicarbonate to remove the remaining flesh and oil. After a rinse in fresh water, they were air-dried at room temperature for 3 to 6 months before being weighed and measured.

Sixty-six of the bacula were from calves less than 1 month old. In that age group, length of baculum ranged from 9.2 to 12.8 cm (mean, 10.6 cm), and dry weights were from 2.7 to 8.1 g (mean, 4.7 g). Data from the bacula of older animals, arranged in order according to their age, indicate that growth in length is rapid in the first 10 years and continues at least to the 15th year (Fig. 22). About 50% of the growth in length takes place by the 5th year and about 90% by the 13th year. In 43 adults that were 15 years old or older, the length of the os penis ranged from 47.6 to 62.2 cm (mean, 55.9 cm); weights (Fig. 22) were from

Table 5. *Relative weights of body parts from Pacific walruses taken March to June, 1958–72.*

	Males[a]		Females[b]	
Part	No. weighed	% live weight	No. weighed	% live weight
Skin and blubber	4	37.9 –49.4	2	27.6 –42.4
Head (with skin, tusks)	4	1.8 – 3.8	2	2.5 – 4.3
Bone and muscle[c]	4	20.6 –40.9	1	26.4
Skeleton[d]	1	4.3	1	3.6
Blood and other fluids	3	8.2 – 8.5	0	—
Heart	5	0.50– 0.56	2	0.80– 0.85
Trachea and lungs	3	1.1 – 1.6	2	1.9 – 2.2
Liver	5	1.5 – 4.0	2	2.8 – 3.2
Spleen	5	0.15– 0.28	1	0.14
Pancreas	2	0.20– 0.37	1	0.25
Stomach (empty)	4	0.49– 0.76	1	0.74
Intestine (empty)	4	2.4 – 3.3	1	3.8
Kidneys	5	0.41– 0.65	2	0.49– 0.63
Adrenal glands	1	0.08	0	—
Penis and testes	2	0.21– 0.38	—	—
Uterus and ovaries	—	—	2	0.8[e]– 2.5

[a] Live weights, 1,225 to 1,557 kg.
[b] Live weights 635 to 914 kg.
[c] Postcranial skeleton and attached musculature.
[d] Skull with tusks, plus postcranial skeleton, thoroughly cleaned and dried (museum grade).
[e] This specimen not pregnant; the other about 1 day postpartum.

489 to 1,040 g (mean, 874.1 g). The longest baculum, from an animal of unknown age, was 62.4 cm; the heaviest weighed 1,070 g. The length of the baculum at birth was about 19% of that in the adult; the weight was about 0.5% of that in the adult (Fig. 23).

In actual size, as well as in relation to the body, the baculum of the adult Pacific walrus is the largest in any living mammal, being equal to about 18% of the standard length and about 0.1% of the whole body weight (Scheffer and Kenyon 1963). It increases 5.3 times in length and about 187 times in weight from birth to adulthood. Its weight:length relationship is divisible into at least four distinct phases of relative growth (Fig. 24), corresponding to the periods of infancy (0 to 3 months), juvenility (1 to 2 years), preadolescence and adolescence (3 to 10 years), and subadult and adulthood (>10 years). The greatest gains in weight per unit of increase in length take place in the first and last phases, which make up the initial period of ossification and the final period of greatest increase in density. In the intermediate phases, the baculum grows relatively more in length than in weight. During the final phase, it is transformed from a relatively slender, spongy bone to one that is stout and strong.

Testes

Testes from 197 animals, including many calves and fetuses, were weighed to the nearest gram, without the epididymides, and their length was measured to the nearest millimeter. Although they usually were slightly unequal in size and

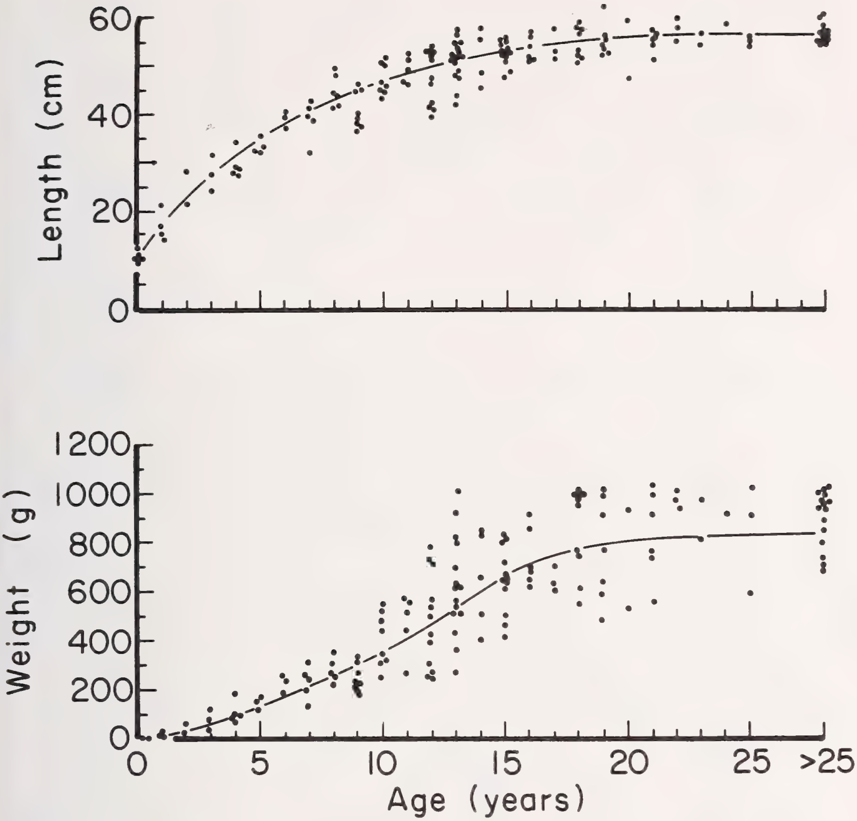

Fig. 22. Length and weight of the baculum of the Pacific walrus in relation to age. Curves were fitted visually.

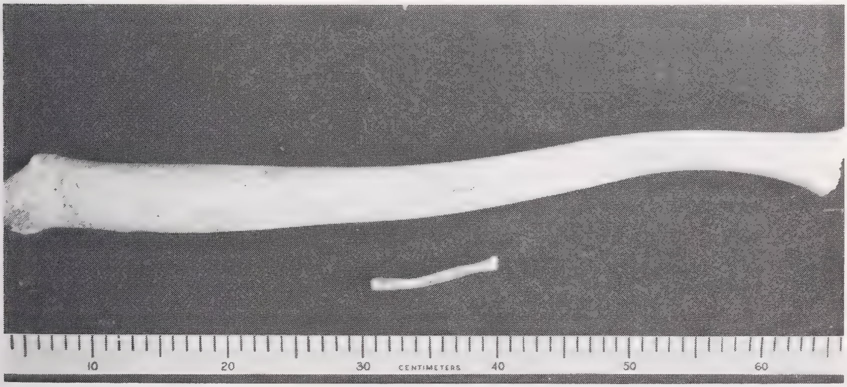

Fig. 23. Comparative size and shape of bacula from a Pacific walrus calf (lower) and mature adult (upper). (Photo by F. H. Fay)

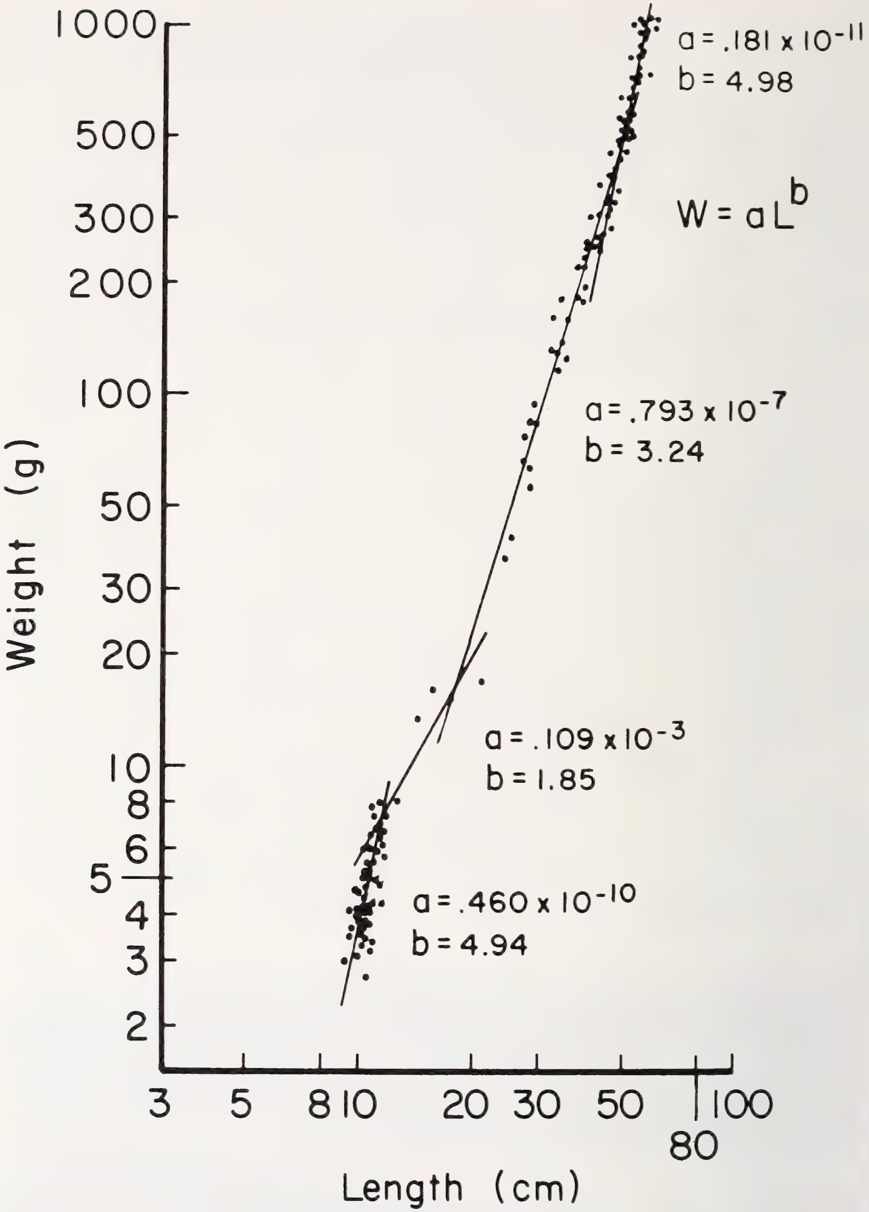

Fig. 24. Weight–length relationship of bacula of the Pacific walrus. The constants for each curve (fitted by least squares) are shown at right.

weight, the differences seldom amounted to more than ± 10%. Weights and lengths reported here are the means of each pair.

The growth of the non-spermiogenetic testis in relation to age is shown in Fig. 25. The length increases steadily for at least 15 years, and the weight for at least

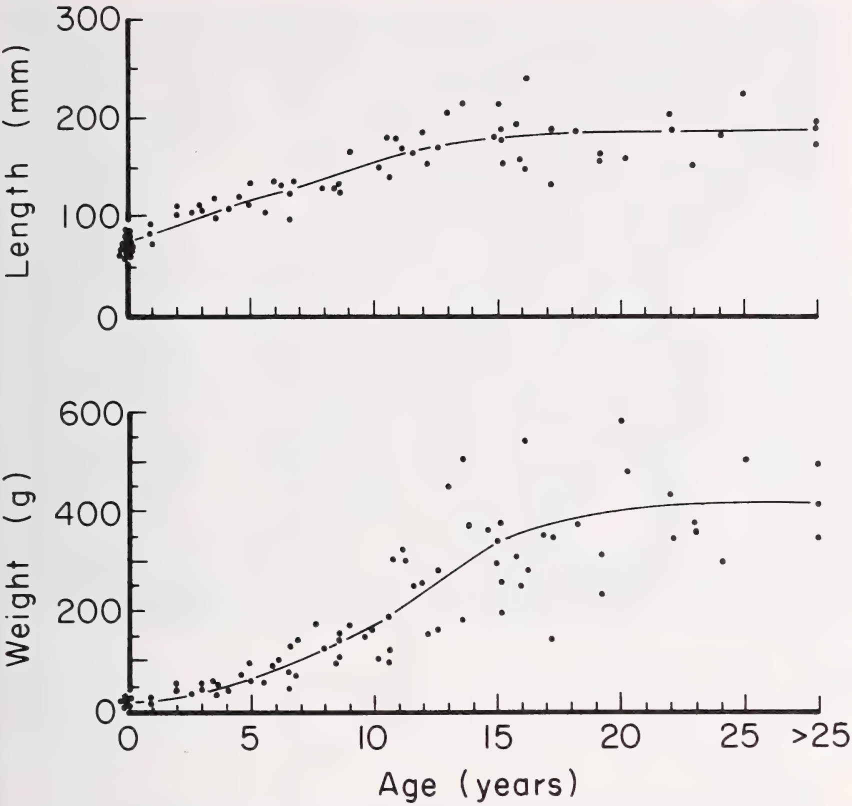

Fig. 25. Length and weight of non-spermiogenetic testes from Pacific walruses in relation to age. Each point represents the mean value of the pair from one specimen. Curves were fitted visually.

20 years. In 64 calves less than 1 month old, length of testis ranged from 60 to 88 mm (mean, 73 mm); weight was from 14 to 26 g (mean, 18 g). The testes of 23 adults 15 years old or older ranged in length from 135 to 240 mm (mean, 188 mm), and in weight from 150 to 584 g (mean, 394 g). During spermiogenesis, the testes of adults increase in length by about 15% and in weight by about 40%.

Os Clitoridis

In the clitoris of the walrus, as in many other mammals (Layne 1954), there is a small mass of bony tissue which is the homologue of the baculum. This bone, the os clitoridis, has not been previously described from the walrus.

In conjunction with collection of data on reproduction in female walruses, I obtained clitorides from 41 calves and 24 older animals to investigate the presence and form of the bone. Upon determining by dissection that bony tissue was present, I boiled each clitoris in 5% sodium bicarbonate solution for about

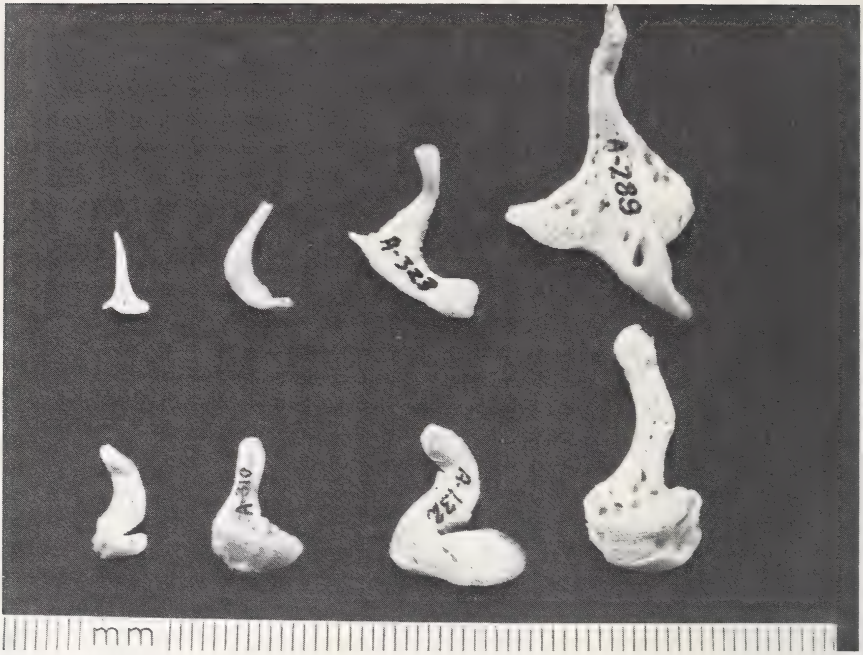

Fig. 26. Variation in shape and size of os clitorides of Pacific walruses. Upper row (left to right) from animals 16, 16, 3, and 7 years old; lower row from calves less than 1 month old. (Photo by K. L. Austerman)

1 h to soften the surrounding tissue and allow removal of the fragile bone. Then, I air-dried the bone for several days before weighing it to the nearest milligram.

A bony os clitoridis was present in 37 (90%) of the 41 calves and in 18 (75%) of the 24 older animals. In the remaining specimens it seemed to be entirely cartilaginous. The ossified specimens were generally S-shaped, but there was wide variation otherwise in their form and size (Fig. 26). In the calves, the bone was cancellous and fragile, and the shaft tended to be circular in cross section. In the older animals, it was more dense and strong but generally more slender and flattened. Overall, there was a trend toward diminution, rather than increase in weight of the bone with increasing age (Fig. 27).

Uterus

The length and diameter of the uterine horns were measured in all of the females that I examined. Length was measured along the anterior curvature, from the middle of the bifurcation to the tubal end; diameter was measured midway of the length. Only nonpregnant and nonparturient animals will be considered here; the enlargement of the uterus in pregnancy and its retrogression after parturition will be described in connection with the reproductive cycle.

The lengths and diameters of the uterine horns in relation to age are shown in Fig. 28. Each point represents the mean for both horns; they rarely differed in size by more than 10%. The estimated growth curves, fitted visually to both sets

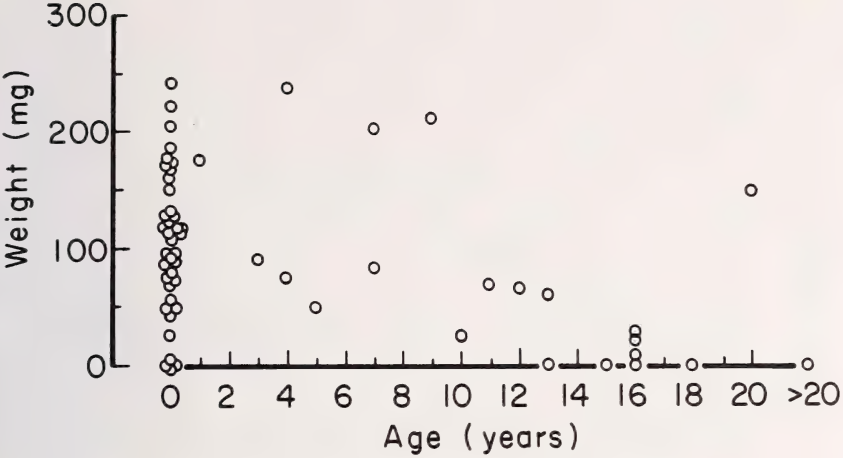

Fig. 27. Dry weight of calcified tissue in os clitorides of Pacific walruses in relation to age. Each symbol represents one specimen.

of data, are sigmoid, and the point of inflection is in the 7th or 8th year. The upper limit of uterine size (average, 22 cm long; 4 cm diameter) seems to be attained usually between the 10th and 12th years and remains more or less constant thereafter. At all stages of development, the diameter of the nonpregnant uterine horns is about one-sixth of the length.

Relation of Physical to Reproductive Development

In the development of body size and weight, as well as of the reproductive organs, the Pacific walrus shows comparable patterns, each of which indicates that full physical and reproductive maturity are attained both actually and relatively later in life in this mammal than in other pinnipeds. Physical development of males is not completed until about 15 years of age, after some 38 to 40% of the maximum life span is past. Although they seem to be reproductively fertile 5 to 7 years earlier than that (Krylov 1967, 1970), they probably are not able to compete for mates until physically mature. The height of the females' physical and reproductive development seems to be reached at about 10 years, although they are capable of reproducing 4 to 5 years earlier (Krylov 1966*b*, 1970). Like many other mammals (e.g., see Montagu 1957; Andersen et al. 1962; Belling 1963; Parsons 1964), their ability to produce offspring is not optimal until they attain full physical maturity. This is an important point to bear in mind, not only from a comparative aspect, but because it has practical relevance to management and manipulation of walrus populations.

The body weights of the males represented in Fig. 21 may be typical only of animals in lean condition. All but three were taken between 9 March and 29 August; the other three (indicated by "W") were taken in late January to mid-February. According to Vibe (1956) and my Eskimo informants, the males tend

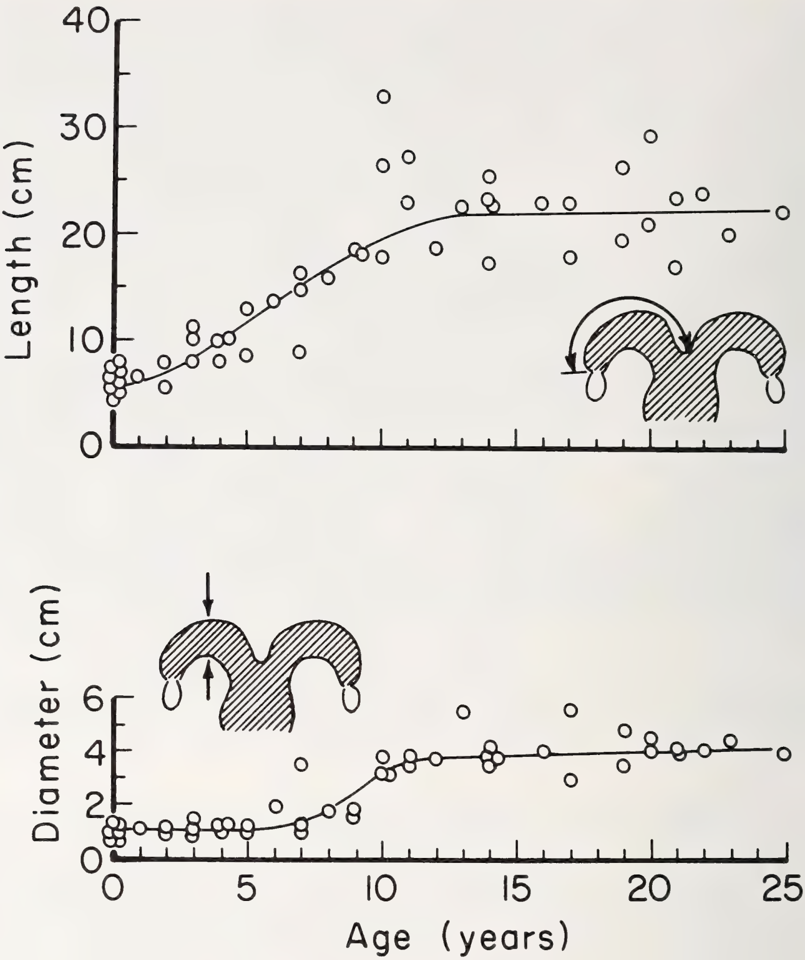

Fig. 28. Length and diameter of the uterine horns in Pacific walruses that were not pregnant and had not recently given birth. Curves were fitted visually.

to be leanest in spring and summer and fattest in autumn to early winter, at which time their blubber may be up to 15 cm thick. If so, the weights shown here may be very conservative. The heaviest male in my series (1,656 kg) was taken in January, and its blubber was the thickest (7.6 cm) of any male that was measured. One of the heaviest males taken in summer (1,557 kg) had only 5.5 cm of blubber, and most of the other, lighter specimens taken at that time had between 2 and 4 cm. By analogy with other pinnipeds in which the "fatted male phenomenon" is known to occur (Laws 1953*b*; Scheffer and Wilke 1953; McLaren 1958; Schusterman and Gentry 1971), adult male walruses can be expected to attain their fattest condition and heaviest weight just before the mating season, which is in mid-winter.

The Eskimos state that the fatness of female walruses varies more with their reproductive status than with the seasons. They claim that the fattest individuals are those that are pregnant with a full-term or near-term fetus in spring. If body weight is proportional to fatness, then the data represented in Fig. 21 lend support to that impression. The weights of mature females (>10 years old) that were pregnant with a near-term fetus in March–April ($N = 10$) were greater ($\bar{x} = 995$ kg, S.E. ±42.4 kg) than those of nonpregnant mature females taken at the same time ($N = 18$, $\bar{x} = 752$ kg, S.E. ±31.3 kg).

Under circumstances as yet unknown, the baculum of the male occasionally becomes fractured. Fifteen examples of fractures were reported by Murie (1936) and four others by Brooks (1954). In my series, only one baculum was fractured, from a specimen about 9 years old. In that animal, the break was about midway of the length, and the broken ends had become slightly dislocated before healing, similar to many of those illustrated by Murie. Murie's specimens were selected as oddities from more than 1,000 walrus bacula collected from prehistoric Eskimo middens on St. Lawrence Island (Geist and Rainey 1936). The others in that series were not fractured (O. W. Geist, personal communication). Brooks' four examples also were from a large series ($N = 180$), the rest of which were not fractured. Thus, the incidence of fracture indicated by Geist's, Brooks', and my samples, combined, was only about 1% (20/1,450). Although even this is a remarkably high rate of occurrence for a condition likely to affect reproductive performance, both Murie's examples and mine suggested that most of the fractures took place at an early age, probably during the period when the bone was increasing greatly in length but not much in density. That is, it seems that most if not all of the fractures are fully healed before the animals attain maturity.

Whereas the baculum increases in size and weight with approach to maturity, its homologue, the os clitoridis of the female, apparently diminishes in size. My findings support the opinion expressed by Mohr (1963) that the frequency of occurrence and the size of the os clitoridis in pinnipeds are inversely related to age. I have found further supporting evidence of these relations in other northern pinnipeds (unpublished data). Most of the published accounts of occurrence and size of the os clitoridis in other mammals also suggest a trend of retrogression with increasing age or reproductive development (see Rinker 1944; Scheffer 1949; Layne 1952; Zeigler 1961; Arata 1965).

Skin and Hair

The skin of walruses is extraordinarily thick and tough and has been likened to that of the African square-lipped white rhinoceros (*Ceratotherium simum*) in both structure and topography (Luck and Wright 1964). Some details of its dimensions and structure, in comparison with the skin of other pinnipeds, were reported by Sokolov (1960) and Ling (1974). The characteristics of the adult pelage were compared with those of other pinnipeds by Scheffer (1964). A few additional points will be covered here, particularly regarding topographic and age- and sex-related characters of the skin and their functional significance. Some new information on the sequence of pelages and molts also will be reported.

My material was obtained from subadult and adult walruses taken in the Bering Sea in January to June, August and December, and from calves taken in April to July. Material from fetuses was obtained from August to January and March to May.

The hair and surface of the skin were inspected in place on the carcasses, and total thickness of the skin (epidermis and dermis) was measured with a metric ruler in incisions at selected locations, taking precautions to avoid distortion of the tissue. Samples for histological study usually were taken several hours after the death of the animal and, in a few instances, after portions of the carcass had been in frozen storage (–10 to –40°C) for several months. Strips of skin, 1 to 3 cm wide and 5 to 10 cm long, were fixed usually in 10% formalin; a few were fixed in acetic-formalin-alcohol (AFA) or in Bouin's fluid. Microsections were prepared from small blocks, mostly about 0.5 cm^3 in volume, cut from the outer surface of the strips. These were dehydrated in ethanol, embedded in paraffin or celloidin, sectioned on a rotary microtome at 7 to 25 μm, and routinely stained with haematoxylin-eosin dye.

General Appearance and Thickness of Skin

The skin of the calf at birth is uniformly leaden gray to gray-brown, and has a thin coat of fine hair, about 5 mm long, of similar color. In the succeeding weeks, the pigmentation of the skin becomes more intense, and the lengthening hair becomes characteristically light brown. By the second week after birth, the hairless flippers are charcoal gray, and the pelage is light reddish-brown; by the end of the third week, the flippers are nearly black and the pelage, now about 7 to 10 mm long, is rusty brown to tawny, as though bleached somewhat by the sun. I noted these changes in calves held in captivity at Gambell during May 1958, 1959, and 1961. Comparable stages were recognized in the calves harvested by Eskimos during the same periods. The contrasting pigmentation of two of those calves, the first about 1 h old and the second perhaps 3 to 4 weeks old, is illustrated in Fig. 29.

The skin probably is more intensely pigmented in these 3- to 4-week-old calves than it is at any subsequent time. At that stage in development, the skin is pigmented at least as much as it is generally in the hair seals (Phocidae) of the Bering–Chukchi region and more intensely than in fur seals and sea lions (Otariidae). With advancing age, the skin of the Pacific walrus becomes progressively paler, as does the pelage. This change is most apparent in the males, whose skin and hair become so lightly pigmented in old age that some individuals appear to be albinistic (Fig. 30). The pallor of such animals is most apparent when they are in the water and for a short time after emergence, when the skin is ischemic. After lying out on ice or land for about an hour in warm weather, they become pinkish to reddish, as the skin is suffused with blood (Ray and Fay 1968). This redness commonly is mistaken for "sunburn."

About 1% of the specimens examined had one or more small, irregular areas of unpigmented skin on the flippers (Fig. 31); these were more noticeable and seemed more common in fetal and newborn than in older animals. Smaller, lightly pigmented to unpigmented spots were common also on the head, neck, and body of most of the specimens examined, but these seemed to be only scars

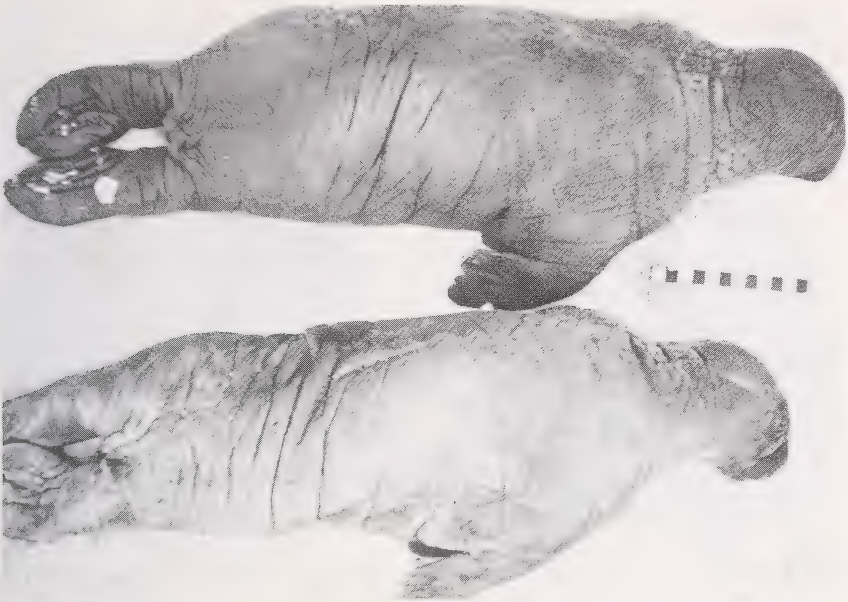

Fig. 29. Comparative pigmentation of the skin on a newborn calf (bottom) and a calf about 1 month old (top). Scale (center) is 30.5 cm. (Photo by F. H. Fay)

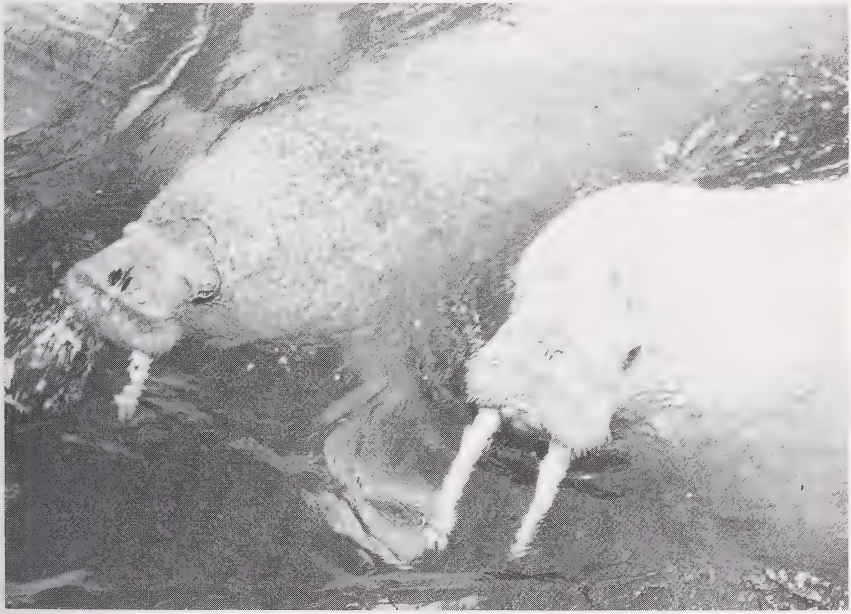

Fig. 30. Comparative pigmentation of the skin on adolescent (left) and adult (right) males, both of which were molting and nearly hairless. The neck of the adult is enlarged, due to partial inflation of the pharyngeal air sacs. (Photo by J. W. Brooks)

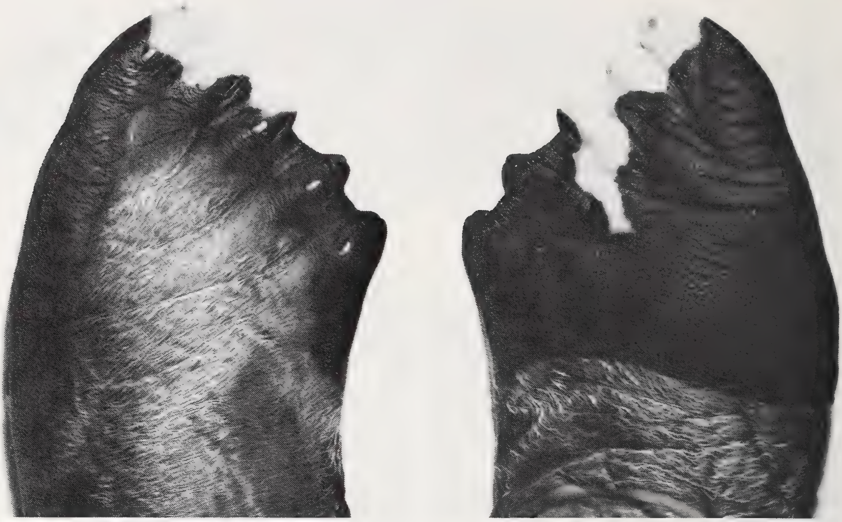

Fig. 31. Pigment-free areas of the skin on the right foreflipper of a Pacific walrus fetus, about 6 months post-implantation. Dorsal (left) and ventral (right) views. (Photos by F. H. Fay)

from superficial wounds. They were most apparent on subadult males.

The skin is greatly wrinkled and folded (Fig. 29), except on individuals that are very fat. These folds develop early in the fetus (Chapskii 1936), as if in anticipation of later thickening of the skin. I presume that their pattern remains more or less constant for the lifetime of the animal, and that it is unique on each individual.

The thickness of the skin (epidermis and dermis) in the specimens that I examined seemed greatest on the neck and shoulders, greater on the dorsal than on the ventral surfaces, and greater in males than in females. These differences were apparent even in small fetuses and were most marked in the adults (Table 6).

The skin is thinnest on some parts of the face and attains its greatest thickness on the neck (up to 40 mm) and shoulders of adult males, where it is supplemented by rounded bosses or "lumps" about 1 cm thicker than the surrounding skin (Fig. 32). These bosses, mostly about 5 to 8 cm in diameter, tend to be hairless and scarred on their distal surface and to have numerous minor cuts and abrasions there. Their internal structure is not remarkably different from that of the surrounding skin, except for extraordinary thickening of the reticular layer of the dermis and minor amounts of scar tissue in the outermost, hairless parts. The total dermal-epidermal thickness of the skin in these bosses may be up to 7 cm according to Brooks (1954), though it is usually about 5 cm.

Freiman (1941) observed that the bosses were absent in males whose zoological length was less than 300 cm, and that they usually were well developed on males whose zoological length was 340 cm or greater. Males less than 300 cm long (standard length <279 cm) are mostly less than 10 years old; those with a length of 340 cm or more (standard length ≥ 316 cm) are mostly 15 years old or older

Table 6. *Regional and age- and sex-related differences in thickness of skin (epidermis and dermis) of some Pacific walruses.*

		Skin thickness (mm) per region					
		Neck		Thorax		Abdomen	
Sex	Age	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral
F	Fetus (Dec)	5.0	—	—	3.0	—	2.5
M	Fetus (Dec)	—	—	3.4	—	—	—
M	Fetus (Jan)	8.0	6.0	7.0	5.0	6.5	5.0
?	Fetus (May)	—	—	11.0[a]	—	—	—
F	1 week	11.8	—	—	—	—	—
F	2 weeks	—	—	—	8.0	—	8.0
?	3 weeks	—	—	—	6.2	—	—
F	1 month	9.0	8.0	8.0	7.0	8.0	6.0
F	3 years	—	—	—	12.7	—	—
F	10 years	—	—	35.0	—	—	—
F	Adult	—	—	—	17.1	—	—
F	19 years	—	—	—	17.0	—	—
F	Old adult	—	—	—	—	—	20.0
M	15 years	—	—	—	27.0	—	—
M	20 years	—	—	—	36.0	—	—
M	26 years	40.0[b]	—	—	—	—	—

[a] Data from G. C. Ray (personal communication).
[b] Thickness between bosses; thickness of bosses was 50 mm.

(Fig. 19). Krylov (1967) observed that the earliest appearance of these bosses is in males 7 years old, and that they are consistently present in males more than 16 years old.

Functional Aspects of Skin

The unusual thickness, strength, and durability of the walrus' skin are functions mainly of the reticular layer of the dermis, in which thick bundles of collagen fibrils form a particularly dense network (Sokolov 1960). It seems likely that the main function of this pachyderma is as a protective armor against the jabs and thrusts by tusks of other walruses. Probably for that reason, the skin tends to be thickest on the dorsal than on the ventral surface of the body, contrary to the "axiom" of greater skin thickness ventrally in pinnipeds, expressed by Sokolov (1960) and King (1964).

In adult males, the normal "armor" is supplemented by secondary thickening in the bosses, mainly on the neck and shoulders. These bosses generally have been regarded as a secondary sexual character that develops as the males approach maturity, presumably by hormonal stimulus (Chapskii 1936; Nikulin 1941; Brooks 1954; Sokolov 1960). Their development in free-living walruses clearly

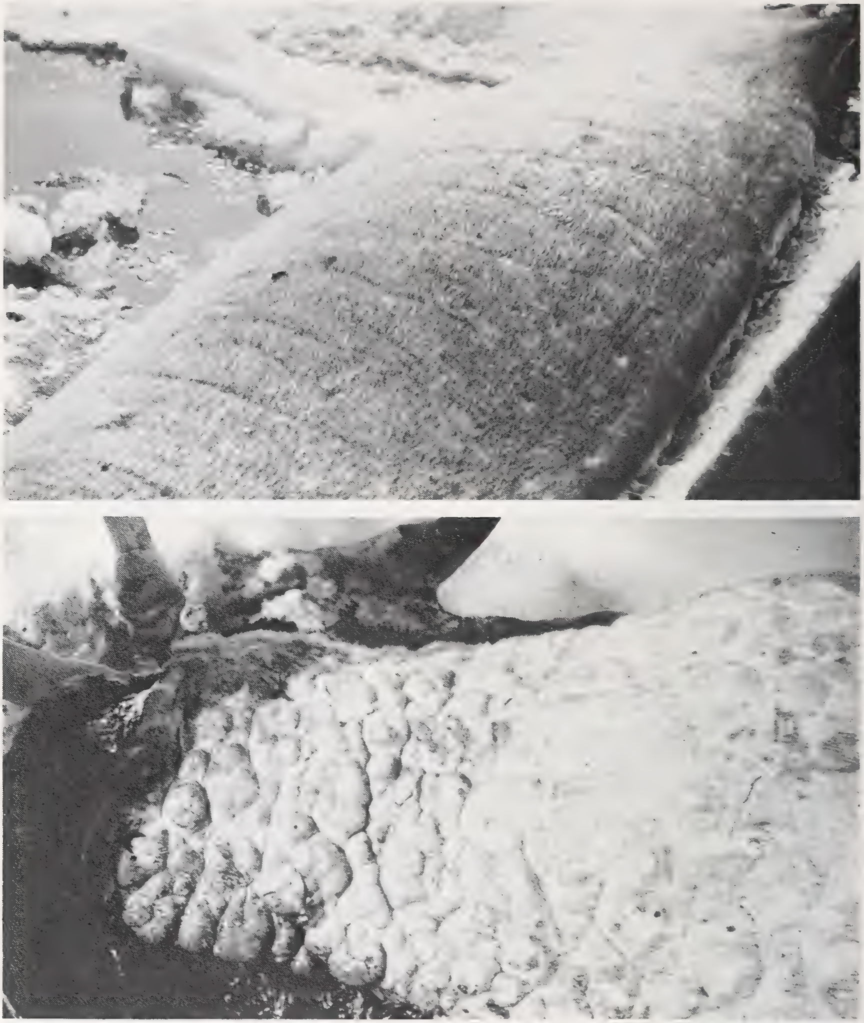

Fig. 32. Pelage and surface topography of adult Pacific walruses: upper — lateral surface of the chest and abdomen of a 15-year-old female; lower — dorsal surface of the neck and shoulders of a 24-year-old male. (Photos by F. H. Fay)

parallels that of the reproductive organs (Krylov 1967). Other investigators (e.g., Brown 1868; Loughrey 1959), however, have regarded them only as scars. Since bosses have not yet appeared in sexually mature male Pacific walruses up to 18 years old that were reared in captivity (E. D. Asper, T. Otten, personal communication), the argument for secondary sexual character is weakened. The evidence for scarring (presumably from tusk-strikes) as a causative factor is much weaker, however, because the females and immature males also are heavily scarred but have no bosses. Furthermore, the bosses on adult males show scar tissue only in their distal, most exposed parts (personal observations). The real cause for their development remains obscure, but I believe that the hypothesis of secondary sexual development is strongest, because the bosses seem to me to have possible social as well as structural value. The thick, nearly hairless neck of the adult male, with its pale, "lumpy" skin contrasts markedly with the more slender, browner, and smoother neck of the adult female and of immature animals of either sex. Hence, it probably serves also as an important visual cue to other walruses of the sex and maturity of the individual.

Blubber

Like other pinnipeds, the walrus has a thick layer of cutaneous fat, the blubber or hypodermis. This layer varies in thickness over different parts of the animal; it is thickest on the torso and thinnest on the head and appendages. According to Sokolov (1960), it is thicker on the ventral than on the dorsal surfaces of the torso, but his sample size was small (three specimens) and he had only two or three measurements from each. His measurements (cm) were as follows:

		"Chest"	"Back"	"Belly"
Adult female	1 October	101	60	—
Young male	23 September	48	34	36
Adult male	22 September	59	—	39

Hence, I question his conclusion.

I measured the thickness of the blubber in a few specimens but only in one location, on the sternum, midway between the forelimbs. Presumably, this measurement is comparable to Sokolov's measurements on the "chest." My goal was to obtain a large enough series from all seasons of the year with which to test the Eskimos' impressions that the males are fattest in winter and that the females are fattest when carrying a full-term fetus. The data acquired thus far (Table 7) are inconclusive.

Epidermal Structure and Topographic Variation

The epidermis of mammals is a stratified squamous epithelium comprising five distinctive layers: germinative, spinous, granular, lucid, and cornified. In only a few samples of walrus skin were all of these strata apparent. The stratum lucidum often was absent; in some instances there was no definite stratum granulosum; in a few specimens, the stratum germinativum was not well differentiated. In two small areas on the ventral surface of the upper lip, I found no stratum corneum. The reasons for these variations and deficiencies are unknown. No relations with sex, age, or season were apparent in my small sample.

In normal section, the epidermis of the Pacific walrus is about 1 mm thick and appears wave-like, with large, primary undulations, the amplitude of which often exceeds the thickness of the tissue itself; smaller, secondary irregularities occur at the dermal–epidermal interface (Fig. 33). Actually, the primary waves are more or less conical, conforming to the major dermal papillae; the secondary

Table 7. *Thickness of the blubber on the sternum, midway between the forelimbs, of some Pacific walruses.*[a]

Age class and sex	Month	No.	Blubber thickness (mm) Range	Mean
Calves				
F	May	3	19–25	22
Adults				
M	January	1	76	–
M	May	2	50–52	51
M	June	3	44–55	48
M	August	1	50	–
F	February[b]	2	51–64	58
F	March[b]	2	36–38	37
F	April[b]	1	33	–
F	May[b]	4	50–76	66
F	May[c]	7	30–102	68
F	June[b]	1	38	–

[a] Data from J. J. Burns, F. H. Fay, and K. W. Kenyon (unpublished data).
[b] Females not carrying a full-term fetus or attending a newborn calf.
[c] Females at full term or having a newborn calf.

irregularities conform to the smaller dermal papillae. Both types of papillae are highly vascularized, particularly at their apices.

The primary epidermal waves in my samples had an amplitude of 0.6 to 1.5 mm and a period of 0.9 to 1.8 mm; the secondary irregularities were from 0.03 to 0.4 mm deep. The outer one-third to one-half of the epidermis comprised 35 to 70 layers of cornified cells that were loosely arranged in animals beginning their molt and very compact in all others. Nuclei were observed only in the inner third of these layers in animals beginning their molt but were apparent nearly to the outer surface in all others.

The greatest departure from that pattern of cornification was seen on the palmar and plantar surfaces of the fore and hind flippers. In each of those areas, the epidermis was from 1 to 3 mm thick, with a cornified layer making up one-half to three-fourths of the total (Fig. 34). The amplitude of the primary waves was from 1.7 to 4.2 mm, with a period of 1.5 to 3 mm, and the cornified layer was densely compacted, with nuclei apparent at all levels. The outermost surface on the crests of the epidermal waves was frayed from abrasion.

Areas of rough, highly cornified skin comparable to those on the palmar and plantar surfaces of the flippers were found also in the front of the mouth, over the premaxillary and mandibular symphyses. There, the epidermis was up to 2.5 mm thick, and the cornified layer made up two-fifths to one-half of the total (Fig. 34). The primary waves were 0.6 to 1.8 mm high with a period of 1.1 to 2.2 mm. The granular layer here was more apparent than in the palms and soles but was only about half as thick. As in the palms and soles, the outermost surfaces of the crests of the waves were greatly frayed from abrasion.

The rugose, highly cornified epidermis on the palmar and plantar surfaces of the walrus' flippers clearly is advantageous for quadrupedal locomotion on land

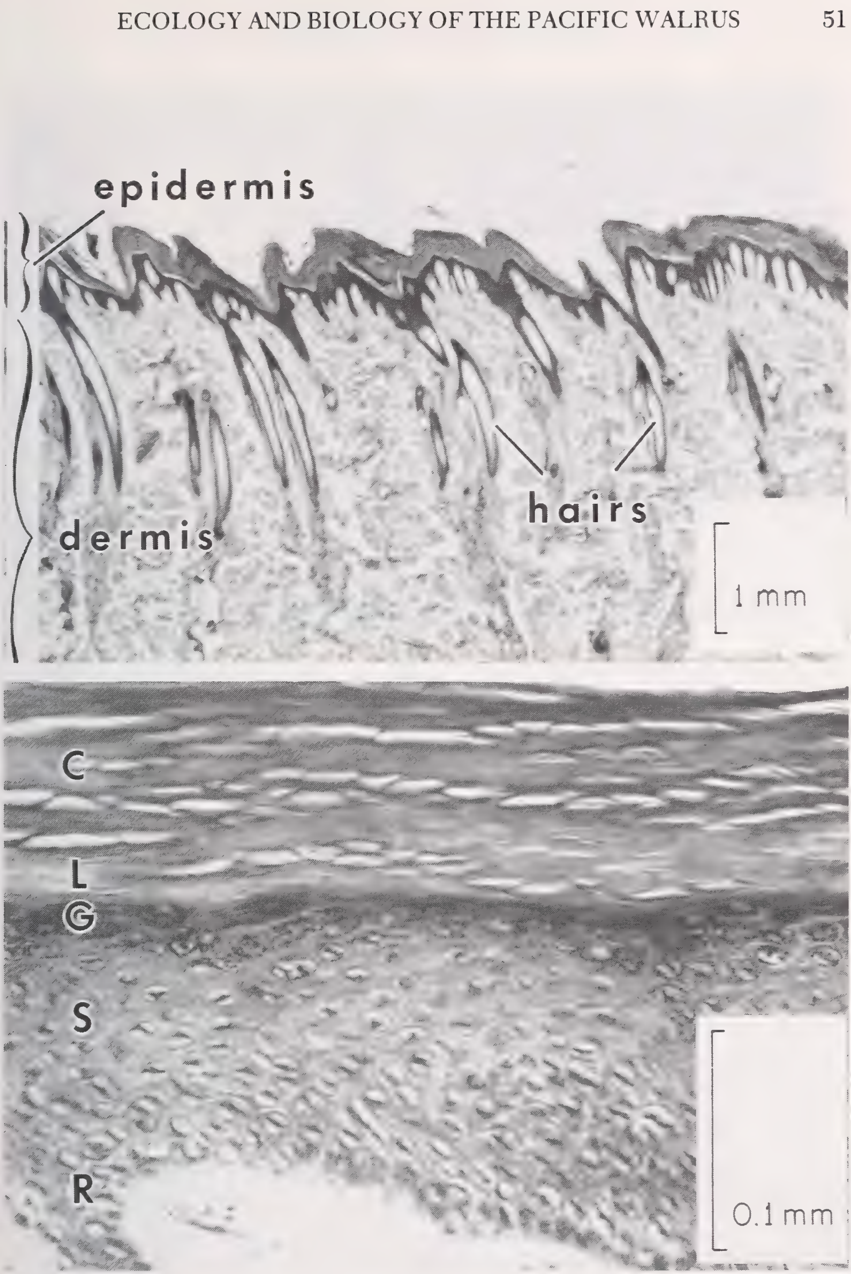

Fig. 33. Longitudinal sections of skin from Pacific walruses, showing (upper) interdigitation of tissues at the dermo-epidermal junction. The five cell layers of the epidermis (lower) are indicated as C = corneum, L = lucidum, G = granulosum, S = spinosum, and R = germinativum. (Photos by S. M. Coulthard and F. H. Fay)

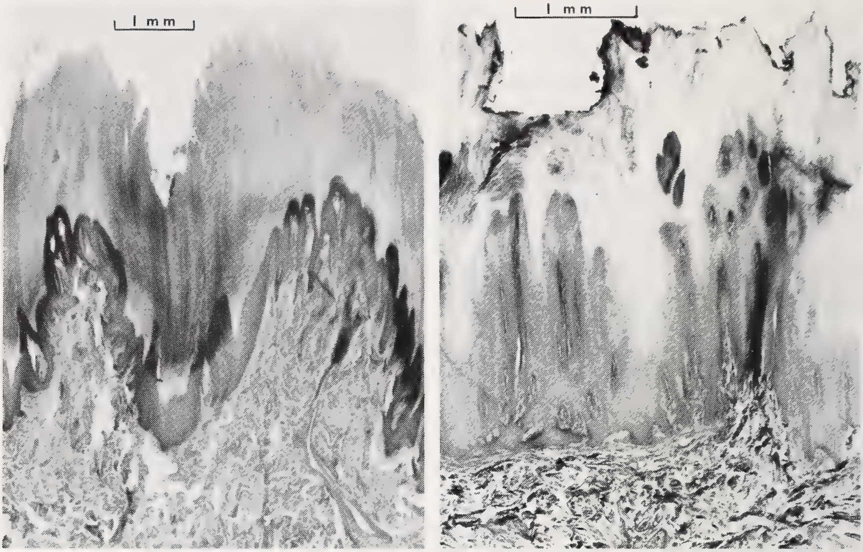

Fig. 34. Longitudinal sections of skin on the palmar surface (left) of the foreflipper of a calf and on the incisive surface (right) of the mandible of an adult. (Photos by S. M. Coulthard)

or ice, as it is in other mammals (Spearman 1964). The presence of similar epidermis on the incisive surfaces of the mouth implies adaptation to requirements for similar protection and adhesive friction. Since teeth generally are absent or vestigial in this part of the mouth, I assume that the rough, cornified tissue serves mainly in grasping and holding prey, during the feeding process. That is, whereas the incisiform teeth perform that function in other pinnipeds, the walrus has nearly lost those teeth in the process of evolution (Repenning and Tedford 1977). In their place, the walrus has developed tough, cornified pads which presumably are advantageous for its unique method of feeding. The importance of this development is discussed further in Food and Feeding Behavior.

I found the cornified layer unusually thick (up to 1.3 mm) also along the dorsal edge of the snout and about the nostrils, whereas it was extremely thin (about 0.125 mm) along the anterior edge of the upper lip (Fig. 35). In the former location, this was parakeratosis but apparently nonpathological, for it was present in all specimens. From the frayed surface of the stratum corneum on the upper edge of the snout, I judge that this area frequently is in contact with abrasive materials, probably while the animal is probing the benthic sediments for food. That is, the heavy cornification there seems to be a normal adaptation that gives added protection to the upper edge of the mystacial pad.

The thinness of the cornified layer on the edge of the upper lip suggests that this is a very sensitive area, important in tactual sensing and selection of food items. On the upper edge of the oral opening, near the corners of the mouth, are two hairless areas, slightly raised and lacking a cornified layer. Nerve bundles

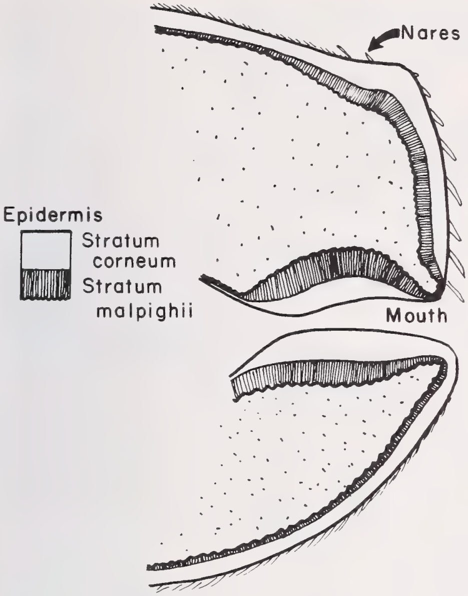

Fig. 35. Diagrammatic representation of the relative thickness of the cornified and Malpighian layers of epidermis on the anterior parts of the face of a Pacific walrus.

are abundant there in the subepidermal tissues, suggesting that these also are particularly sensitive areas.

Pilosebaceous Units

Each pilosebaceous unit on the body usually comprises a single hair with several sebaceous glands and one apocrine sweat gland (Sokolov 1960). The sebaceous glands are compound, and each empties into the hair canal through a separate duct. Well-developed sweat and sebaceous glands were present in the skin of fetal walruses in their first (lanugo) pelage, some 6 months before birth. In those specimens, the opening of the sweat duct into the pilary canal always was distal to the openings of the sebaceous ducts.

The sweat glands of adult walruses taken in autumn and winter were of small diameter and apparently inactive. Atrophy of the sweat glands in autumn was recognized earlier by Sokolov (1960). In all of the calves and older animals taken during the spring and summer, the sweat glands were capacious and apparently productive. In most of my specimens, the ducts entered the hair canal at the same level as or somewhat distal to the entrance of the slightly convoluted sweat duct; in a few, the sweat duct was slightly more distal.

Some of the largest sweat glands, with a capacity at least twice that of glands on the body surface, were found in the anterior surface of the snout, where they were associated with groups of small hairs in the spaces between the mystacial vibrissae. Conceivably, these larger glands function in the production of scent that is important in olfactory recognition during the nose-to-nose greeting between mother and calf and between older animals (see Miller 1976). Sweat and sebaceous glands were absent from the hairless skin of the fore and hind flippers but were present in the hairless “sensory” areas of the oral opening. In these sensory areas, a thick, almost granular exudate was excreted from the slender clusters of sebaceous glands; the sweat glands there were greatly reduced and apparently not functional.

In the haired skin of walrus calves and adults, the ducts of the sweat and sebaceous glands generally open into the hair canals at the same, rather than at different levels. Conversely, in the body skin of the Otariidae, the nearest relatives of the walruses, the orifice of the sweat duct is by far the more distal; in most of the Phocidae, the sweat orifice tends to be the more proximal (Ling 1965). The significance of this difference between the otariids and phocids, in relation to phylogeny and function was discussed recently by Ling (1965) and Mitchell (1967). Both investigators recognized that there are interspecific and topographic variations in the positions of the ducts in both groups, but concluded that the more proximal position in most Phocidae probably is functionally related to the less dense pelage. On that basis, the walrus might have been predicted to have sweat orifices more proximally situated than those of any other pinniped, since it is the most sparsely haired of all (Scheffer 1964). My finding that the sweat orifice is consistently distal to those of the sebaceous ducts in fetal walruses implies phyletic relationship to the Otariidae (recently confirmed by Tedford 1976, and Repenning and Tedford 1977). The shift in relative positions of the ductal orifices before birth implies pre-adaptation to the sparsely haired condition in later life. One can infer from this that ancestral walruses were more densely haired than those living today, and that the trend toward sparser pelage is a relatively recent development, convergent on the Phocidae. Because the shift in position of the ductal orifices takes place rather late in fetal development, it may be a recent adaptation that is still under way.

Pelages and Molts

Prenatal Pelage and Molt

In four fetuses with crown–rump lengths of 10.6, 13.2, 17.8, and 18.6 cm, taken in August, minute primordia of pelage hair follicles were present in the skin on the torso, neck, and head; those on the cheeks, snout, and lips were further advanced in development than any others. In the next larger fetus, 20.8 cm in crown–rump length and taken in September, elongate hair canals and primordial sebaceous glands were present. In a 28.5-cm fetus, taken in early October, about 3.5 months post-implantation, hair cones of the first (lanugo) pelage were developing.

Seven fetuses taken near the end of November and in the first half of December (5.5 to 6 months post-implantation) had a dense coat of fine whitish to silvery hair and well-developed mystacial and superciliary vibrissae (Fig. 36). Crown–rump lengths of these specimens ranged from 45 to 63 cm. The pelage hairs, 3 to 6 mm long, were very slender, sinuous, and circular to elliptical in cross section. They contained no medulla and only traces of pigment, usually in the distal third of the shaft. Generally, a single hair was present in each hair canal. When there were more than one per canal, the hairs arose from branched follicles of about equal length and were virtually identical, hence not classifiable

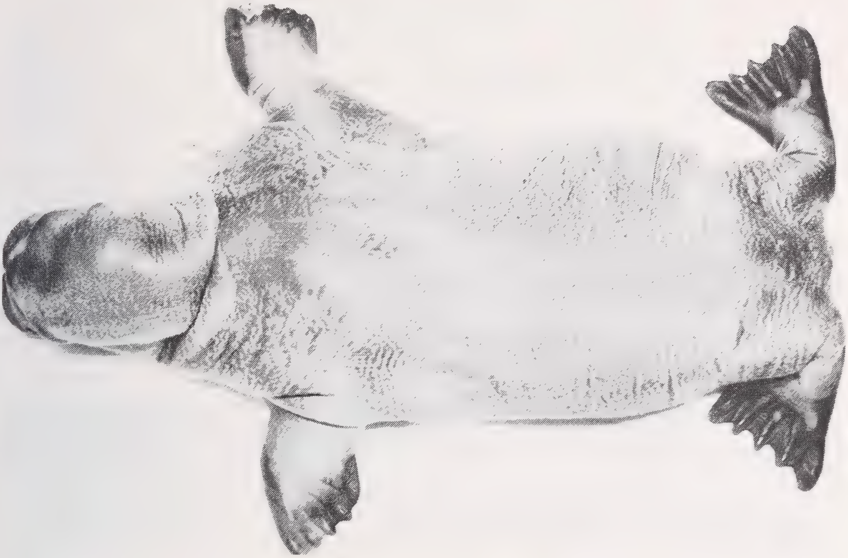

Fig. 36. Dorsal view of a Pacific walrus fetus, about 6 months post-implantation (length about 70 cm). The damp lanugo pelage lies in a rippled pattern, nearly flat against the skin. Dark areas on the flippers are hairless. (Photo by F. H. Fay)

as guard hairs and underfur. The dimensions and appearance of the hairs are compared with those of the subsequent pelages in Table 8 and Figs. 37 and 38.

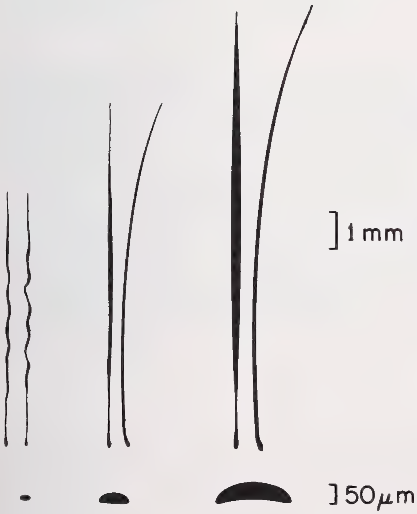

Fig. 37. Comparative size and shape of primary hairs of the lanugo (left), natal (center), and adult (right) pelages of the Pacific walrus. Upper row, anterior and lateral views of single hairs; lower, cross-sectional shape, midway of the blade.

Table 8. *Size of primary hairs and numbers of hairs in three pelages of the Pacific walrus.*

	Length (mm)		Diameter (μm)			Density	Pores (%) with different numbers of hairs		
Pelage[a]	Exposed shaft	Root	Basal	Medial	Distal	(no./cm^2)	1 hair	2 hairs	3 hairs
Lanugo	3–6	1–2	13–16	20–30	4–6	2,200–2,400	89	10	1
Natal	5–10	2	26–36	21–83	3–6	680–1,260	91	9	<1
Adult	7–12	3	35–105	55–231	20–30	113–142	92	8	<1

[a] Data from two specimens in each pelage.

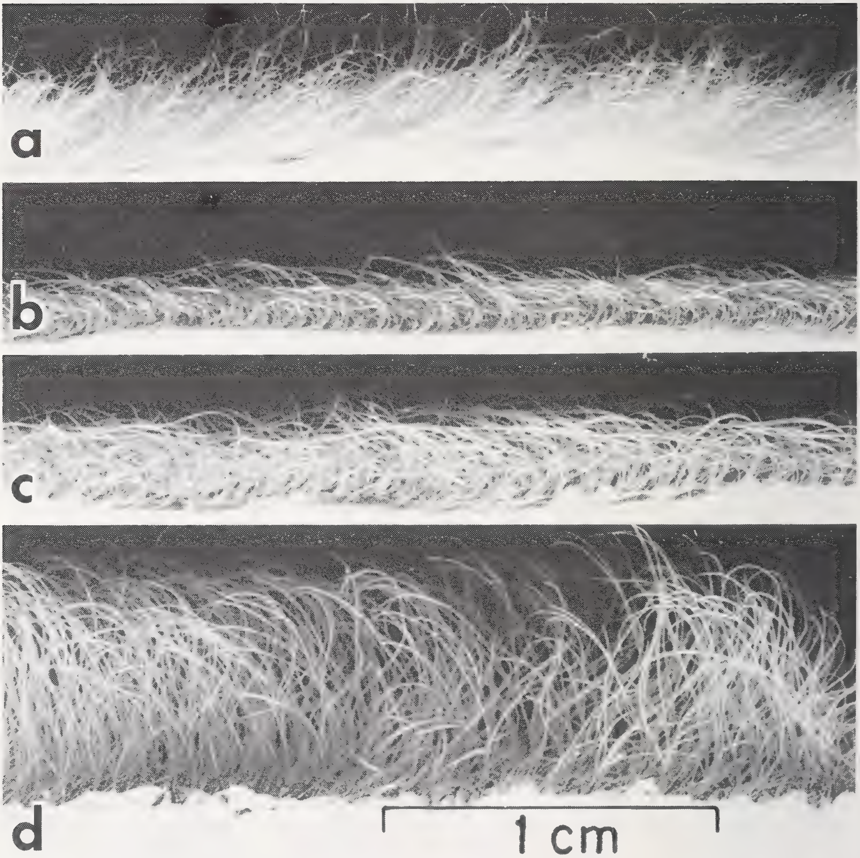

Fig. 38. Comparative appearance of the pelages of the Pacific walrus, as seen in sagittal sections of dried skins: (a) lanugo, at 6 months post-implantation; (b) natal, at birth; (c) natal, about 1 month after birth; (d) adult female. Anterior at left, posterior at right. (Photos by G. C. Kelley)

Hairs plucked from the body surface of these seven fetuses were club-rooted. Histological sections from the body skin of two of the fetuses, a male taken 6 December and a female taken 15 December, showed pelage hair follicles in retrogressive (catagen) and resting (telogen) stages, respectively. Samples of meconium (fecal material) from the colon of each of these two specimens were washed in tap water and examined for shed hairs. Because the meconium comprises cells and other debris ingested by the fetus with the amniotic fluid, hairs that are shed by the fetus also will appear there. In about 10 cm^3 of this material from each specimen, a total of two broken vibrissae and nine pelage hairs of the type just described were found. The presence of so few shed hairs and only of the types already present on the specimens indicated that the white, wavy coat was the first (lanugo) pelage and that it was the product of the follicular cycle whose beginning was seen in the smaller fetuses.

The next older fetus, taken in mid-January (7 months post-implantation), had a crown–rump length of 56.5 cm and was shedding its lanugo. Coarser, brownish hair was present on the head, neck, chest, back, and belly and mixed with the white lanugo on the flanks and shoulders. White hair of the first pelage was present alone in the axillae, on the limbs, and about the umbilicus. Histological sections from each of those locations showed shallow-rooted club hairs of the first pelage and deeply rooted, actively growing, pigmented hairs of the second pelage. Sweat and sebaceous glands were well developed, and all of the sweat ducts entered the hair canals distal to the sebaceous ducts. White, wavy hairs of the first pelage were abundant in the meconium. Maceration of the meconium in an aqueous solution of sodium hydroxide (to remove the cellular debris) yielded a dense, white felt of lanugo hairs, identical in dimensions and pigmentation to those of the younger fetuses.

I examined superficially 11 fetuses taken in late March, none of which showed any outward traces of the lanugo. The hairs of their second pelage extended 2 to 3 mm above the surface of the skin. Histological preparations from two of these fetuses, taken on 23 and 24 March, about 9.3 months post-implantation, showed deeply rooted hairs of the second pelage in late catagen and early telogen.

The last group of fetuses was obtained in April and May, at or near full-term development. Ten of these were examined superficially, and three were examined histologically. The hair on each fetus was straight to slightly curly, nonmedullated, heavily pigmented in the distal third of the shaft, and extended 3 to 5 mm above the surface of the skin. In cross section, each hair was elliptical near the base; in the distal two-thirds of the shaft, it was broadly lenticular; distally, each hair tapered to a fine point 3 to 6 μm in diameter. Histological sections showed the hairs to be club-rooted and in catagenetic and telogenetic follicles. There was no evidence of new growth or of the fine hairs of the lanugo pelage. The fine hairs, however, were abundant in the meconium.

The pelage of calves up to 1 month old was identical to that of the full-term fetuses, except that it extended 1 to 2 mm farther above the surface of the skin. Apparently, this increase was due only to the hairs having migrated outward slightly during late telogen, after the club-root was fully formed. Each pilary unit included a capacious sweat gland and several small sebaceous glands. The duct of each sweat gland entered the hair canal at the same level as or slightly distal to those of the sebaceous glands, as in the full-term fetuses.

Postnatal Molt of Calves

Data presented by Nikulin (1941: Table IV) from inspection of 53 calves indicated that shedding and replacement of the natal coat takes place in June and July, about 1 to 2 months after birth. Information and materials obtained in the present study confirm that observation.

No outward signs of shedding or newly emerging hair were seen in more than 100 calves examined during May; histological sections of skin from a few of these showed only resting follicles. In one specimen, about 2 weeks old, a few hair bulbs were somewhat enlarged and descendant but lacked the intensely pigmented hair cones typical of anagen; the stratum corneum still was compact (Fig. 39a). In a second specimen, about 1 month old, hair cones were present, and the stratum corneum was greatly expanded and loose (Fig. 39b). However, the natal pelage of this animal still was firmly anchored, and there were no outward signs of depilation. Of 10 calves taken in early June, 3 showed bald areas on the crown and midline of the back; the natal hairs adjacent to those areas were loose and club-rooted. Incisions in the skin of one of those specimens, taken 2 June, disclosed intensely pigmented hair shafts of the not yet emergent third pelage and a loose, easily detachable cornified layer. In the remainder of this group, there were no bald areas, and the natal hair still was relatively firm.

Samples of skin from the body of four calves taken on 27 July indicated that the animals were about midway through their postnatal molt. Most of the natal hair already had been shed, and the remainder was loose and easily pulled out. New hairs of the third pelage extended 0.5 to 2 mm above the surface of the skin, and the intensely pigmented hair cones were still open and actively growing. The thick, cornified layer of the epidermis was intact in some areas, though loose and easily rubbed off (Fig. 39c); elsewhere, its outer portion, about 0.2 mm thick, already had been shed (Fig. 39d). This material was detaching as flakes, 1 to 3 mm in diameter.

The date of completion of the postnatal molt is unknown. From the specimens described above, I presume that the new hairs do not become club-rooted earlier than mid-August to late August and that they probably do not attain their full emergence above the skin before the end of that month. Chapskii (1936) reported that the calves he saw in August to October had a short, fine pelage, but no measured lengths were given. Mansfield (1958*a*) observed that the pelage of calves taken in "summer and fall" in northern Hudson Bay was only 1 to 2 mm long.

The progress of the postnatal molt in 13 calves reared in captivity in North American zoological gardens was followed on the basis of external appearances and reported to me (personal communication) by D. H. Brown (Marineland of the Pacific), W. P. Heuschele (San Diego Zoo), and G. C. Ray (New York Aquarium). First indications of shedding of the natal coat were noted between 2 and 14 June; the first appearance of new hair was recognized between 11 June and 7 July, and the new (third) pelage was regarded as fully developed by 19 to 26 July. These reports indicate that the postnatal molt takes place more rapidly in captives at mid-latitudes than in free-living calves under arctic conditions.

The previously accepted notion that the natal coat of the walrus was its first pelage (see Nikulin 1941; Brooks 1954; Mansfield 1958*a*) was questioned by Scheffer (1958:11), who suggested that the natal coat was the "dark second

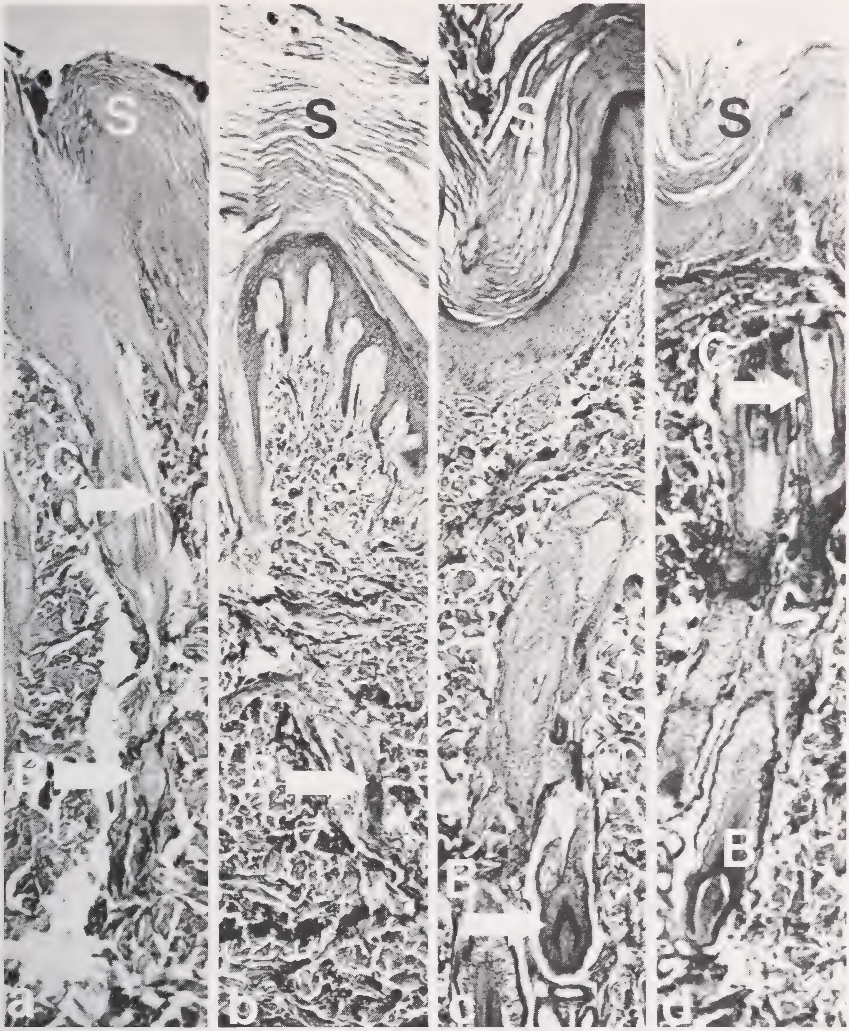

Fig. 39. Sagittal sections of skin from the top of the head of Pacific walrus calves, showing stages in the postnatal molt: (a) at 2 weeks after birth, with compact stratum corneum (S), elevated club roots (C) of the second (natal) pelage, and quiescent, unpigmented hair bulbs (B); (b) at 1 month after birth, with loosening stratum corneum, club roots of the natal pelage still in place, and hair bulbs becoming pigmented; (c) at 2 months after birth, with hair bulbs descendent and enlarged; and (d) at 2.5 months after birth, with most of the stratum corneum shed, some natal hairs still in place, and hairs of the third (postnatal) pelage heavily pigmented, deeply rooted, and growing. (Photos by G. C. Kelley)

pelage" and that the "whitish fetal coat" had been lost in the course of the walrus' evolution. As I have shown in the foregoing account, the predicted whitish lanugo has not yet been lost, though it is of rather short duration and is shed well

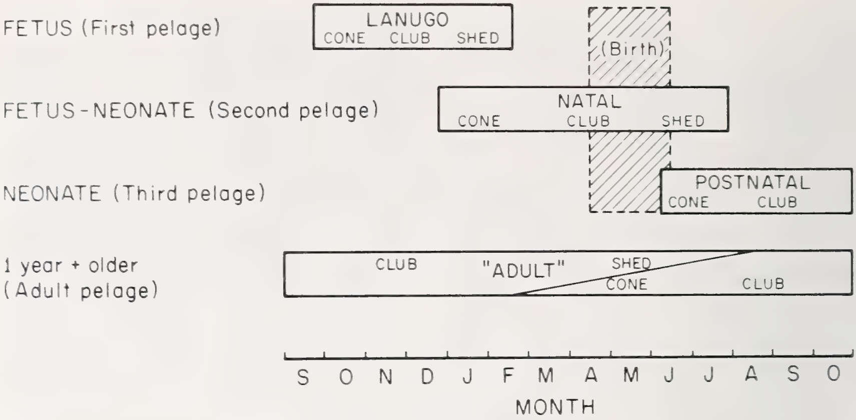

Fig. 40. Sequence of events in development of the lanugo, natal, and post-natal pelages of Pacific walrus fetuses and calves, in relation to the annual molt of adult-type pelage in the older animals.

before the time of birth. This is different from the lanugo of Phocidae but somewhat like that of the northern fur seal (Otariidae), if Belkin's (1964) analysis is reliable (see below). This first (prenatal) pelage is markedly different from the later pelages of the walrus, in form as well as in pigmentation. In general, the hairs resemble underfur, rather than guard hairs, except that they usually occur singly rather than in bundles. To some extent, the first pelage resembles that of other pinnipeds, in that the hairs are fine, sinuous, and largely unpigmented (cf. Belkin 1964; Stutz 1966). The second (natal) pelage closely resembles that of the adults, except that the hairs are somewhat shorter and less robust. The third (postnatal) pelage is essentially the same as the second.

The walrus may be the only pinniped that bears three different pelages and undergoes two true molts within 1 year of fetal to early postnatal life (Fig. 40). Although Belkin (1964) indicated a similar schedule of events in the northern fur seal, true molt of the white lanugo before development of the natal coat was not detected by Scheffer (1962) in his scrupulously detailed study of the fetal pelage of that species. On that account, and because of some doubts about timing, Ling and Button (1975) have questioned Belkin's results.

Pelage and Annual Molt of Adults

The pelage of adult walruses is coarser and less dense than that of the calves (Table 8; Figs. 37 and 38), yet it imparts the same furry or velvety appearance to the body surface (Fig. 32). When dry, the hairs are erect and the tips tend to curve forward, hiding from view most of the topographic details of the skin; when wet, they lie flat against the skin. On the bosses of the neck and shoulders of adult males, the hair often is very sparse or absent, exposing the surface of the skin to view (Fig. 32).

More than 90% of the hair canals of adults bear only a single primary or guard hair; canals with more than two hairs are scarce (Table 8). Where two or three hairs occurred per canal, one usually was much larger than the other(s); the small hairs were otherwise exact replicas of the large hairs and not readily classifiable as secondary hairs or underfur. Each small hair arose from a separate follicle but emerged with the larger hair from the same hair canal. The hairs extended 7 to 12 mm above the skin over most of the body but generally were shorter on the face (4 to 8 mm). They were intensely pigmented in the distal third of the shaft in the youngest animals and were virtually colorless in some very old adults. As in the Phocidae, the hairs lacked medullary air spaces, though the shafts were stouter than those of the medullated guard hairs of the Otariidae (Sokolov 1960; Scheffer 1964). The pelage hairs of adult walruses were similar in shape to those of the newborn calves. However, they were stouter and longer, and the blade was more lenticular in cross section (Table 8; Figs. 37 and 38).

The annual molt in most adults seems to be more gradual than the postnatal molt of the calves, beginning at least 1 to 2 months earlier and continuing well into the autumn; mixed populations of both the new and the old generations of hair are present during most of the molt's course (A. W. Mansfield and J. J. Burns, personal communication). Although I noticed no outward signs of growth of new pelage hairs in any of the animals examined during March to early June, histological preparations of skin from the top of the head of one female taken on 31 March showed hair follicles in anagen. Skin from the crown of three others taken at the same time showed only resting follicles. Another taken on 14 May also had follicles in anagen.

J. W. Brooks and K. W. Kenyon (personal communication) observed that a few adult males taken in Bering Strait about mid-June already had shed much of their hair. Bailey and Hendee (1926) found new hair "underneath the loose epidermis" in animals taken in the same locality during June and July. Most of the old, cornified layer had been shed from a male that I examined at Gambell on 27 August. Mixed populations of old and new hairs (ratio about 1:3) over most of its body were remarkably short (less than 4.5 mm), the old hairs having been broken and the new hairs not completely emerged. The follicles of the new generation of hair were still in late anagen. Mansfield (1958*a*) observed that some new hair on adults was up to 12 mm long by August, but that some old hair was retained at least as late as October in walruses of the Canadian Arctic.

Indications of a more rapid, and perhaps more thorough, molt in animals at the southern edge of the summer range were recognized by J. W. Brooks, K. W. Kenyon, and me on 23 to 27 June at Round Island. There, all but a few of the oldest bulls had shed virtually all of their old hair (Fig. 41), and about one-third of the animals already had a coat of new hair a few millimeters long. The nakedness of males that probably were undergoing a comparable molt was noted in another southern locality, the Pribilof Islands, by Elliott (1875:160) on 5 July. He also observed that "the thick, yellowish-brown cuticle . . . seemed to be scaling off in places." At Round Island in June, shed hairs and flakes from the cornified layer were abundant on the beaches and rocks where the animals had lain. Although the further progress of this molt has not been closely followed, photographs taken in August of animals (presumably the same ones) on the beaches of Round Island (Goro 1960) showed them in a fully developed, though perhaps not fully emergent, new pelage.

Total depilation, followed by total replacement, seems to be the rule also in

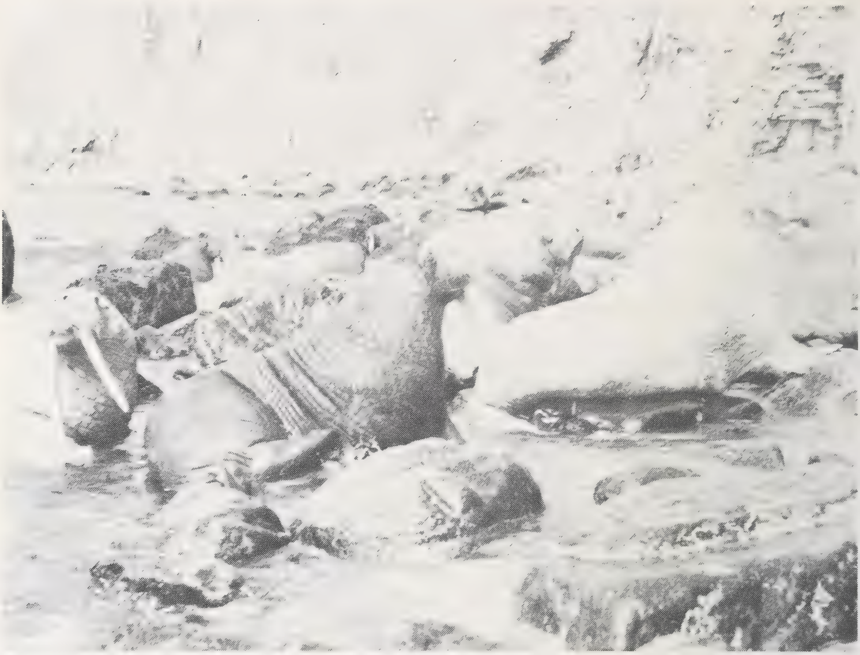

Fig. 41. Molting male walruses at Round Island, Bristol Bay, on 24 June. These animals had shed most of their hair, exposing the surface of the skin to view. The deeply pigmented skin of the adolescent male at center contrasts in color and topography with the pale, knobby skin of the adults around him. (Photo by K. W. Kenyon)

walruses in captivity at lower latitudes. Reventlow (*in* Mohr 1952) reported that two animals, about 1 year old, in the Copenhagen Zoo began shedding in mid-May and had "beautiful new 'pelts' again" by 25 June. This pattern has been observed also in North American zoological gardens (D. H. Brown, G. H. Pournelle, and G. C. Ray, personal communication). In eight specimens ranging in age from 1 to 10 years, shedding of the old hair usually was apparent in May (Fig. 42) or at the latest by early June, and the new pelage was everywhere emergent, though perhaps not fully developed, by the end of June.

Molt Process

The annual molt in the adult walrus seems greatly protracted, relative to that in other sparsely haired pinnipeds, evidently beginning in some individuals as early as March and continuing in others as late as October. The peak of shedding and replacement of hair and of cornified epithelium seems to be in July and August, about the same time as the postnatal molt of the calves. However, the timing of the molt appears to differ between animals in the northern and southern parts of the range, and the loss and regrowth of hair seem more rapid in the latter than in the former. Furthermore, the annual molt in captive walruses

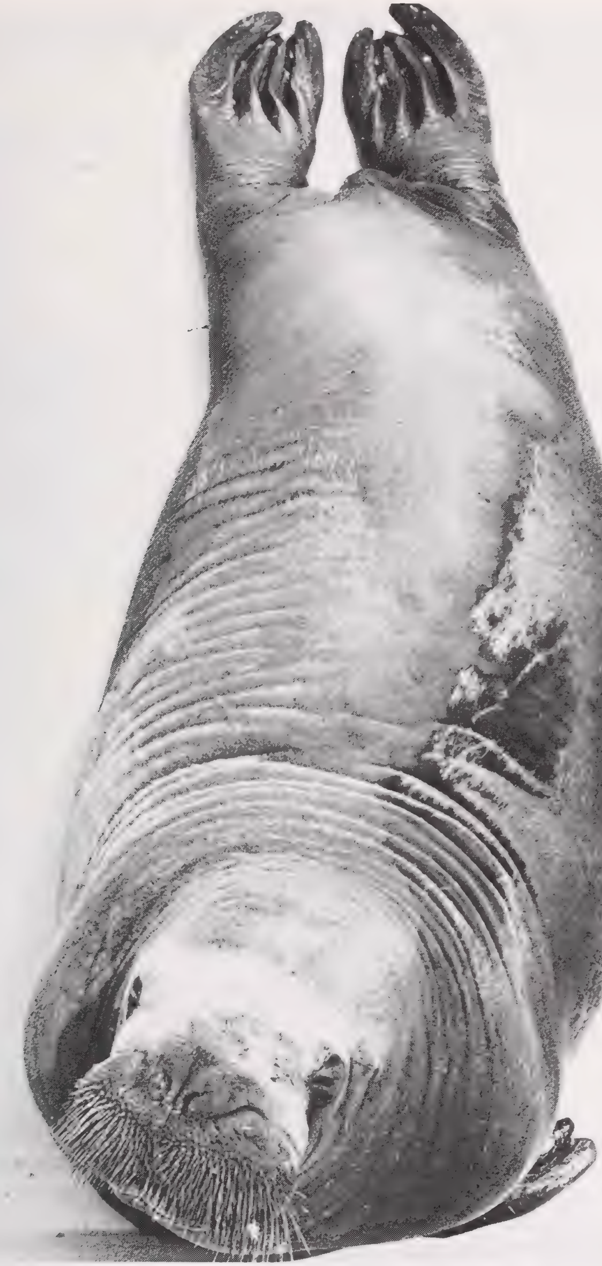

Fig. 42. Molt in a 2-year-old Pacific walrus at the New York Aquarium. The old pelage remains in place on the sides, is being shed along the back, and is being replaced by new hairs on the head. (Photo by G. C. Ray)

in the temperate zone evidently begins and ends much earlier than that of any of their free-living counterparts. More information is needed to clarify these points, but their implication is that the annual molt is triggered as much by thermal as by photoperiodic stimuli.

The possibility that heating and suffusion of the skin with blood were of major importance in accelerating the molt of pinnipeds first occurred to me at Round Island in June 1958, when I observed that the walruses having most of their pelage intact showed complete depilation about their partly healed superficial wounds. At the same time, the animals which already had shed most of their hair showed fully developed new pelage hairs about their healing wounds. Because, in my experience, wound-healing is associated with both congestion and heating by blood, I suspected that the more rapid molt about the walruses' wounds was facilitated by those two factors, which are closely linked in these mammals (Fay and Ray 1968; Ray and Fay 1968).

That the growth of hair and other epidermal appendages of mammals is accelerated by warming and hyperemia and is depressed by cold and ischemia has been reported in many other contexts (e.g., Haddow et al. 1945; Hale 1945; Storey and Leblond 1951; Montagna 1956; Héroux 1960; Sapin-Jaloustre and Sapin-Jaloustre 1956 *in* Héroux 1960). Although one might expect the epidermis of walruses to be enzymatically adapted for metabolism and growth at low temperatures, my observations of hair growth about healing wounds and more rapid and complete molts at Round Island than farther north, were contraindicative of such adaptation. When the walrus is immersed in the cold water of the Bering and Chukchi seas at about –2 to +10°C, its skin is about as cold as the surrounding medium and is generally deprived of blood (Fay and Ray 1968). At those temperatures, the cutaneous cells of walruses and other pinnipeds seem to be incapable of proliferation (Feltz and Fay 1966). When the animal emerges from the water and is warmed by the ambient air and solar radiation, the skin is suffused with blood. The provision of both heat and nutrients apparently allows the epidermal cells to proliferate. The greater the heat and suffusion, as with decreasing latitude or increasing amount of time spent on the haulout, the more rapidly the molt seems to be completed.

Facial Vibrissae

The pinnipeds possess three kinds of facial vibrissae: rhinal, superciliary, and mystacial. Rhinal vibrissae occur only in certain phocids (Ling 1966, 1977); the superciliaries are prominent in phocids but weakly developed in otariids (Scheffer 1962); the mystacial vibrissae are highly developed in all pinnipeds. None of the walruses that I examined possessed any rhinal vibrissae or vestiges thereof, but I found superciliary vibrissae often in fetuses and newborn calves. These usually numbered one or two (rarely three) above each eye, and sometimes attained a length of 1 cm. They rarely were noticeable in animals more than a few weeks old, but I did not determine whether their apparent absence was due to their having been shed or merely abraded or broken off. The mystacial vibrissae, however, were well developed in all of the specimens that I examined, and I saw no evidence of their ever being shed or replaced. Mohr (1950) and Yablokov and Klevezal' (1964) reported that they range in number from about

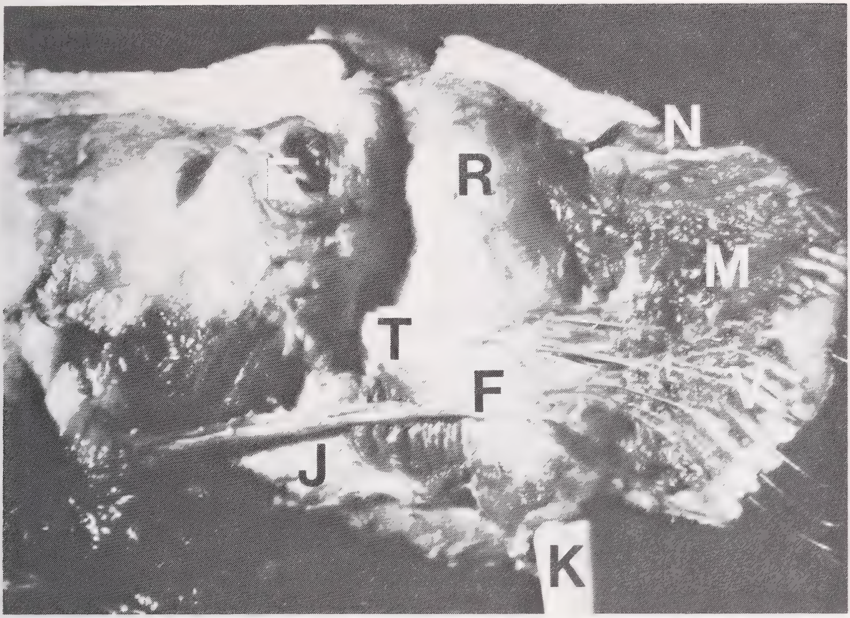

Fig. 43. Innervation of the mystacial vibrissae and snout in a 4-year-old Pacific walrus. Skin and part of musculature removed from the right side of the face, exposing the eye (E), jaw (J), external nares (N), and the bone surrounding the root (R) of the tusk (K). Large branches from the facial (F) and trigeminal (T) nerves enter the proximal end of each vibrissa (V); other branches enter the intervening rostral musculature (M). (Photo by F. H. Fay)

400 to nearly 700 per walrus and are situated in 13 to 18 rows on the anterior surface of the rostral pad. I counted them in one adult female and found 468. According to Kosygin (1975*b*), the mean number per side is slightly greater in males (242.48 ± 4.65) than in females (223.68 ± 3.05).

The mystacial vibrissae of the walrus have a smooth surface and are oval in cross section; the ratio of least:greatest diameter is about 3:4. In the adult, these hairs are whitish to yellowish and translucent, with an opaque medulla in which there are no air spaces. The root of each is enclosed in a stout capsule of connective tissue, to which many fine strands of striated muscle are attached. Within the capsule, the hair is surrounded by a series of sinuses, typical of sensory hairs. The upper and lower blood sinuses are relatively smaller and the ring sinus and *Ringwulst* relatively larger than those in the elephant seal (*Mirounga*) described by Ling (1966).

The principal nerves serving the vibrissae and the muscular rostral pad are the maxillary branch of cranial nerve V (trigeminal) and the dorsal buccal branch of cranial nerve VII (facial). Both of these are unusually large in the walrus, and their fibers combine partially in the vicinity of the tusk socket (Fig. 43). From that point, they radiate into the rostral pad, sending a large branch to the proximal end of each vibrissa follicle and others to the intervening muscles and skin.

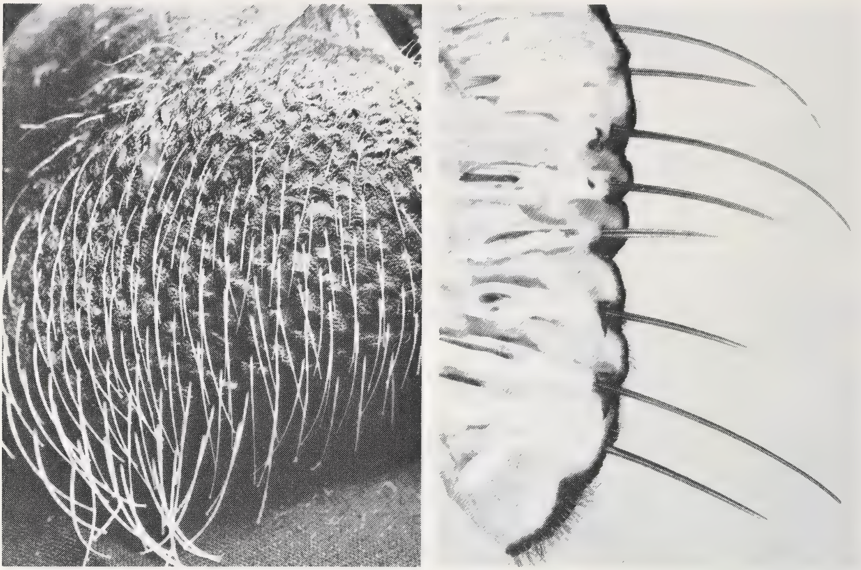

Fig. 44. Mystacial vibrissae of a fetus (left) 6 months post-implantation, and of a calf (right) about 1 month old. In the fetus (right anterior view), the tips of the slender, unpigmented vibrissae are blunt and frayed, whereas those of the stout, pigmented vibrissae of the calf (sagittal section of snout skin) have been rounded by abrasion. (Photos by F. H. Fay and G. C. Kelley)

The mystacial vibrissae are the first hairs to appear in the fetus. Some were present in my youngest specimen, 1.5 months post-implantation, in which the primordia of the pelage hair follicles were not yet fully differentiated. The fetal vibrissae are soft, white, and opaque, and more slender and curly than those of calves. In the fetuses, the vibrissae on the upper part of the snout usually were the shortest and most slender; those in the lower lateral quadrants were longest and stoutest. Most of them curved downward and inward, toward the mouth or chin, and the tips were blunt (broken) or frayed (Fig. 44).

The mystacial vibrissae of newborn calves were like those of the fetuses, but within 3 to 4 weeks after birth they were appreciably stouter, apparently having grown considerably in that time. The root and proximal part of the shaft were heavily pigmented in these older calves, and the tips were worn smooth, rather than frayed or broken (Fig. 44). Maximum basal diameters of the larger vibrissae ranged from 0.9 to 1.2 mm. Some in the upper lateral quadrants of the snout were worn down to the level of the surrounding skin; the rest were about three-fourths as long as those in newborn calves.

Most mystacial vibrissae present in 1-year-old animals were nearly twice as stout but about half as long as those of the calves. They were whitish at the tips, grading to dark brown at the base, those in the uppermost rows being palest. The tips were smoothed or beveled, as a result of abrasion, and a large proportion of the vibrissae in the upper third of the snout was worn down to or below the level of the surrounding skin. In progressively older animals, the vibrissae tended to be

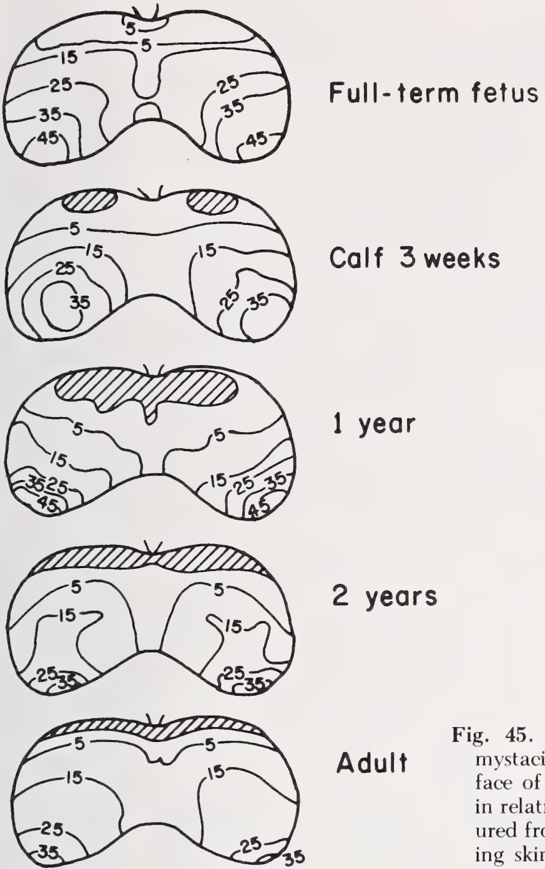

Fig. 45. Isograms of length (mm) of mystacial vibrissae in the anterior surface of the snout of Pacific walruses, in relation to age. Lengths were measured from the surface of the surrounding skin. Crosshatched areas indicate lengths less than 1 mm.

stouter and paler but usually not any longer than those of the 1-year-old young. The largest vibrissae in a 4-year-old male had basal diameters of 2.2 to 2.5 mm; those of an adult female were 2.5 to 2.9 mm.

The topographic variation in length of vibrissae on the anterior surface of the snout in several walruses of different ages (Fig. 45) shows that in each specimen, the shortest hairs were situated near the upper edge of the snout and the longest hairs near the ventrolateral edges. This pattern was virtually the same in all individuals more than 2 years old, though the actual lengths varied widely. The length of each vibrissa is a function of its rate of growth and rate of decrement by abrasion. The result of growth alone is seen in the fetus, where length increases continually, except for breakage of the tips. It is seen also in certain individuals raised in captivity, an outstanding example of which was shown by Mohr (1950: Fig. 2). Such animals often develop very long vibrissae, unlike those of walruses under natural conditions, but the basic pattern of relative lengths is nonetheless similar (Fig. 46).

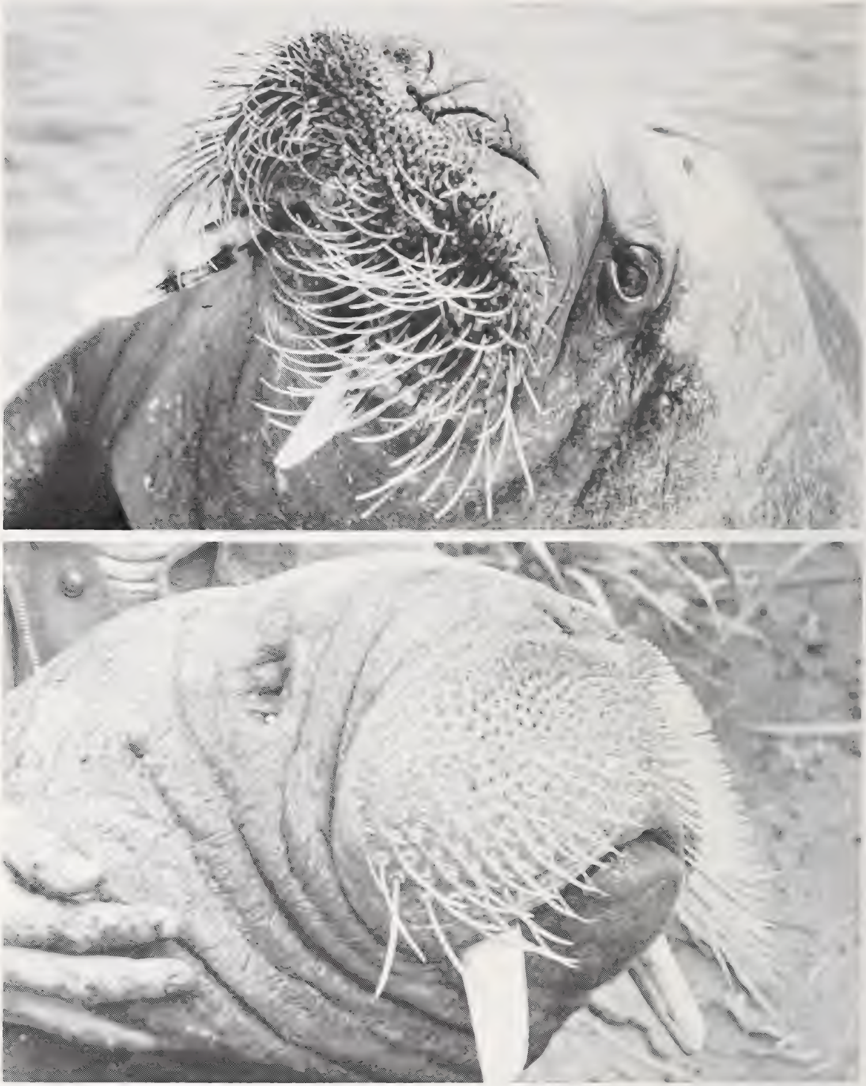

Fig. 46. Comparative lengths of mystacial vibrissae in captive (upper) and free-living (lower) walruses. Both animals were immature males. (Photos by G. C. Ray and K. W. Kenyon)

That the vibrissae of wild walruses are kept short by continual abrasion seems to have been recognized first by Allen (1880:29). Nikulin (1941) concluded that the abrasion takes place in connection with feeding, specifically from contact with abrasive bottom materials while the animals dig up mollusks with their tusks. Questioning this, I investigated the abraded surfaces of the vibrissae in all parts of the snout and in specimens of a wide variety of ages. My findings follow.

First, abrasion of the vibrissae takes place not only in the older animals that feed on benthos, but also in very young calves which have no tusks and whose diet consists entirely of milk. The vibrissae of the young calves evidently grow continually. At the same time, they become appreciably shortened and rounded soon after birth and, in two areas high on the anterior surface of the snout, become worn down to the level of the skin. From observations of calves under natural conditions, as well as in captivity, I concluded that the reduction in length of their vibrissae occurs principally by abrasion during their search for the mammary nipples. This search seems to be more by tactual than by visual means: while brushing their mustache vigorously and forcefully over the mammary area with a sort of "rooting" motion, the greatest frictional force is applied to the dorsal edge of the snout. The abrasive surface, in this instance, is the coarse skin and hair of the mother. The resulting areas of minimal vibrissa length increase in extent with advancing age and usually coalesce medially before the animals are 1 year old (Fig. 45). At that age, the infant walrus still is dependent on a milk diet, though probably supplements it occasionally with mollusks. When the young walrus is weaned, at 18 to 24 months, the area of minimal length attains its maximal breadth, extending to the lateral edges of the snout. This pattern is sustained to adulthood.

Second, the vibrissae on the anterior surface of the snout are most intensively abraded on their dorsal side. In the uppermost rows, the tips are steeply beveled; vibrissae farther down show a progressively more oblique bevel (Fig. 47). Along the upper edge of the snout, where the vibrissae are worn shorter than the surface of the surrounding, highly cornified skin, their tips are abraded squarely or slightly rounded. The few vibrissae posterior to the upper edge of the snout are abraded mainly on their anterior surface; those farthest posterior tend to be the longest and most obliquely beveled (Fig. 47).

These findings indicate that the greatest and most direct frictional force, perpendicular to the surface of the skin, is applied along the upper edge of the snout. The incident angle of contact with abrasive materials is progressively more acute and less intense ventrally and posteriorly from that area. Close inspection of the abraded surfaces of the vibrissae indicates further that the direction of motion of the abrasive particles contacting the front of the snout is from dorsal to ventral, for example as might occur with a "rooting" motion of the head—the same motion used by the calves when seeking the mammary nipples. This kind of abrasion is the reverse of that predictable from digging with the tusks. In digging, the relative motion of the abrasive particles would be from ventral to dorsal and would tend to abrade the vibrissae more on their ventral than on their dorsal surfaces.

Vibrissal Function

The dense population of mystacial vibrissae in the walrus identifies the broad snout as an organ of extreme tactual importance. The theory expressed by Sokolowsky (1908) and Brehm (1926:319) that these vibrissae serve as a kind of food-sieve, in the manner of the baleen plates of mysticete whales, was rejected by Mohr (1950), because the vibrissae are on the outside rather than the inside of the mouth, and because they rarely attain sufficient length to cover the mouth.

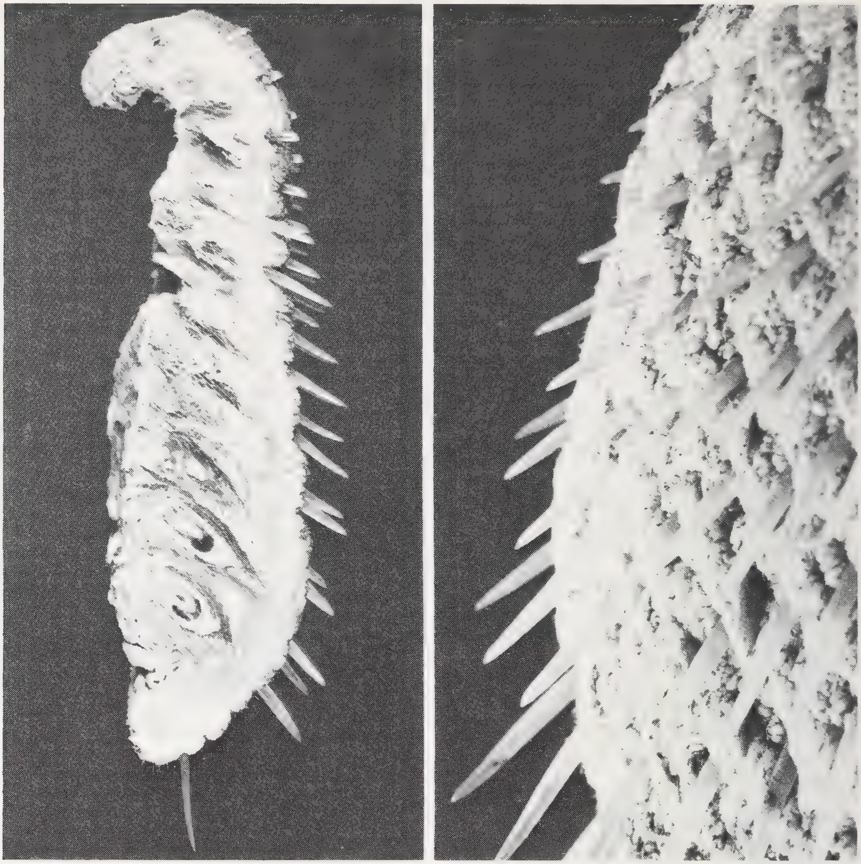

Fig. 47. Differential abrasion of mystacial vibrissae of Pacific walruses, in relation to their location on the snout: left, median sagittal section, with dorsal edge of snout at top; right, oblique anterodorsal view, upper right quadrant. (Photos by G. C. Kelley and F. H. Fay)

She recognized that long vibrissae would be more of a hindrance than an aid to the walrus, due to obstruction of the oral passageway. She concluded that their main functions were sensory and that they were used for expressing changes of mood. Howell (1930:77) stated that the walrus forces food into its mouth by "medial contraction" of the rostral pad, and that a captive walrus was said to have used its vibrissae to tear the flesh from a dead seal. Sokolowsky (1908) and Nikulin (1941) indicated their belief that the mustache is used as a "broom" to sweep together the food unearthed by the tusks. Brooks (1954:24) believed that the pad and vibrissae performed both motor and sensory functions during feeding, " . . . serving to sort out clams and like food from the muck stirred up by the tusks." Social functions of the vibrissae for expressing threat and submission, were described by Miller (1975*b*).

My opinions on the function of the vibrissae in feeding were derived mainly from observation of free-living and newly captured calves in the Bering Sea, and from observation of eight captive walruses in the New York Aquarium, Marineland of the Pacific, and Sea World–San Diego. Although the behavior of walruses reared in captivity is not necessarily comparable to that of free-living animals, it is at least indicative of the extent of their capabilities.

I found the rostrum and its vibrissae extremely mobile. Each vibrissa can be moved up, down, and laterally, and can be rotated through at least 100° of arc, such that the tips can be turned upward and inward, toward the center of the snout, as well as downward and outward. During feeding or in exploration of unfamiliar objects, the pad and mustache were extremely active and were capable of directing selected objects toward the mouth while pushing others away. In my opinion, the mystacial pads of these captive walruses were at least as effective as two hands in sorting, selecting, and manipulating materials, and they performed those functions in a very rapid and efficient manner. I saw no signs of the mustache being used either as a filter or as a "broom" (in the mechanical sense), or as a battery of "claws" for tearing apart flesh. In both the free-living and the captive calves, as well as in the subadults and adults in the three aquaria, the entire mustache often was used more as a tactile "broom" for exploring surfaces of other animals, rocks, ice, and unfamiliar objects than as a mechanical device for sweeping. The head often was lowered and raised repeatedly, with the vibrissae in contact with the explored object, and the whiskers were in motion only during the raising of the head. I assume that this was the kind of action interpreted earlier as having a sweeping function.

The most extreme abrasion of the vibrissae along the upper edge of the snout correlates well with the greater protective cornification of the skin there than elsewhere on the face. Also the angle of incidence and direction of movement of the hard particles that abrade the vibrissae correlate well with those in the abrasion of the tusks, as will be shown in the section on dentition. These relations, plus the powerful levating musculature of the head and neck, all point to frequent and strenuous use of the snout as a digging or "rooting" organ.

Dentition

The dentition of the walrus was studied by several leading anatomists and naturalists of the 18th and 19th centuries, with particular concern for dental homologies and descriptive dental formulae. In a review of their work, Allen (1880) noted a certain lack of accord on the dental formulae but observed that the problem of homologies of the upper and lower incisors and of the lower canines had been solved. The dental formulae were revised further in the present century by Cobb (1933), based in part on reinterpretation of the earlier work and in part on his own observations. Cobb also described in detail the dental morphology and structural peculiarities of the skull which he considered to be associated with the method of feeding and the development of the tusks. Cobb's report has been the accepted standard reference on the dentition of modern walruses for 50 years.

In connection with my investigation of methods for age determination, I examined also the ontogeny and succession of the teeth, as well as their morphology, structure, growth, and function. Many of my findings contribute to further understanding of those aspects and relate especially to current questions of phylogeny, anatomy, development, and feeding.

Definitions

The principal references consulted in connection with these studies were Kronfeld (1937), Schour (1953), and Scott and Symons (1961). The terminology used here is as follows:

- A *primary tooth* is a tooth of the first or "milk" dentition; it has no antecedent. Primary teeth are indicated by lower case letters: i, c, p, and m.
- A *secondary tooth* is a tooth of the second or "successional" dentition; it is a tooth that has a primary antecedent. A secondary tooth usually develops on the lingual side of its primary antecedent and eventually replaces it. Secondary teeth are indicated by capital letters: I, C, and P. There are no calcified secondary molars.

The teeth are designated as incisors, canines, premolars, and molars. Starting from the anterior midline of the upper and lower jaws, they are identified as follows:

- The *incisors* (i, I) are the only teeth in the upper tooth row that are rooted in the premaxillae; in the lower tooth row they are the only teeth anterior to the canines, from which they are usually separated by a diastema slightly greater than the spaces between the incisors themselves. Except for I^3, all of the incisors of the walrus are very small, vestigial teeth and usually are resorbed early in life.
- The *canines* (c, C) are the largest and most deeply rooted teeth. The upper canines, situated anteriormost in the maxillae and lateral to the main tooth row, are called *tusks* because of their large size. The lower canines are aligned with the premolars and usually are slightly longer rooted but of about the same diameter.
- The *premolars* (p, P) are the postcanine teeth that antecede (primary) or are replaced by another tooth (secondary) during dental succession.
- The *molars* (m) are small, vestigial teeth, situated posterior to the premolars and often separated from them by a slightly wider space than that between the premolars themselves. These are the last teeth to develop in the primary dentition, and they are the only primary teeth that are never replaced by secondary successors. They usually are recognizable by the fact that their roots are slightly offset laterally from the secondary tooth row.

The surfaces of a tooth are: *lingual* toward the tongue, *labial* toward the cheeks and lips, *occlusal* toward the opposing teeth, and *apical* about the root apex.

A tooth is said to have a *crown* and *root*. The *anatomical crown* is the part with an outer covering of *enamel*. The *anatomical root* is the rest of the tooth, proximal to the anatomical crown and having an outer covering of *cementum*.

The *clinical crown* is the entire distal part of the tooth that is exposed beyond the gingiva. It may comprise not only the anatomical crown but part of the anatomical root, as well. The *clinical root* is the remainder of the tooth, proximal to the gingiva.

Eruption is the gradual emergence of a tooth out of its alveolus or socket, until the anatomical crown is fully exposed. *Alveolar eruption* is the emergence of the crown above the rim of the bony socket. *Gingival eruption* is emergence of the crown above the gingiva. *Distad migration* is the further movement of the tooth, after the crown is fully erupted. When a tooth is gingivally erupted to the extent that it touches any of the teeth in the opposing tooth row, it is said to be in *occlusion* with its *antagonist.* When the mouth is closed to the extent that the fully erupted teeth meet, the dentition is said to be *occluded.*

Each of the developing primary and secondary *tooth germs* lies in a spacious *follicle* of soft tissue, which is entirely or partly within an open pocket in the bone. This pocket is the *alveolus.* The term "crypt" is not appropriate in the walrus, since no follicles are completely enclosed by bone. Later, when the development of the tooth is well advanced, the root is enclosed in a tightly fitting bony *socket,* to which it is attached by fibers of the *periodontal membrane.*

The proximal end of the root is the *root apex,* in which is an aperture, the *apical foramen.* Through the apical foramen pass the neural and vascular connections that serve the dental *pulp.* The pulp is a soft, gelatinous tissue situated within the *pulp chamber* of the clinical root. Its peripheral cells (odontoblasts) produce the *dentin* which makes up most of the body of the tooth. Over the outer surface of the clinical root, *cementum* is deposited by cementoblasts of the periodontal membrane. The production of calcified dental tissues by odontoblasts and cementoblasts is known as *apposition.* It comprises the formation of successive layers of organic matrix and deposition therein of calcium salts. Growth of the tooth is therefore by *accretion,* i.e., it is cumulative from addition of *increments* laid down upon those already present. This is in contrast to the intussusceptive growth of most bones and other tissues, wherein new material is formed among that already present. The calcified dental tissues are permanent, to the extent that their structure and composition are not modified during further development of the tooth. However, they can be removed (*decrement*) by several processes: *attrition* is a wearing away at the locus of contact with opposing teeth; *abrasion* is by frictional contact with materials other than the opposing teeth; *fracture* occurs especially in the tusks from percussive contact with hard objects or excessive torque; *resorption* is the chemical removal of tissue by osteoclasts of the periodontal membrane. I have seen no evidence of dental caries (cavities) in walrus teeth.

Ontogeny of Primary and Secondary Dentitions

The teeth of *Odobenus* are in a dynamic state of evolutionary change, as is evident from their extreme irregularity in occurrence, size, and position. This variation has led to marked controversy among naturalists as to dental homologies and the proper descriptive notations for the walrus' dental formulae. I investigated the ontogeny of both the primary and the secondary dentitions in some detail in a series of small fetuses provided by A. W. Mansfield and J. J.

Burns and several larger fetuses and older animals that I obtained at Gambell. As a result of that investigation, I was able to identify several teeth that had not been recorded previously in the walrus and to contribute to solution of some of the previously controversial problems.

The specimens examined were 15 fetuses, ranging in age from about 1.5 to 6 months post-implantation, 38 calves and full-term fetuses, and 135 other animals that were from 1 to more than 30 years old. Of the smallest fetuses, seven were stained with alizarin red S, macerated in potassium hydroxide, and cleared and mounted in thermal plastic or in glycerol. In three of these, only half of the head was stained and cleared; the other half was serially sectioned. The dentitions of two other fetuses and four calves were examined roentgenographically in lateral oblique and ventral views and, subsequently, by dissection. The dentitions of four fetuses, nine calves, and 15 older animals were studied by gross dissection and subsequent examination of the cleaned, dried skulls. Other specimens, examined in the field, were 60 cleaned and dried skulls and 78 fresh heads with the soft tissues still intact. In the fresh specimens, I recorded only the gingivally erupted teeth.

In young fetuses, up to 6 months post-implantation, the presence of a dental follicle, alveolus, or both was accepted as evidence of a developing tooth, even when calcification was not detected. The "dentitions" of such specimens are described by a "follicle formula," to distinguish them from the actually calcified teeth of older specimens. The dental formulae of the older specimens include only those teeth that were represented by calcified tissue.

Primary Teeth

The formula for the complete primary dentition of the walrus is

$$i\frac{1\text{-}2\text{-}3}{1\text{-}2\text{-}3}\ c\frac{1}{1}\ p\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\ m\frac{1\text{-}2}{1\text{-}2} \times 2 = 38.$$

None of the specimens that I examined had this full complement; the maximum in any one specimen was 34 teeth, lacking only m^2 and m_2. However, these "missing" molars were found in other specimens whose dentitions were incomplete in other respects. My designation of the lower premolars here as 2-3-4, rather than 1-2-3, is new and is based on my observations that (1) they are the only primary postcanine tooth follicles that are succeeded by secondary teeth, (2) all three develop into relatively stout, well-calcified teeth, as do $p_{2\text{-}3\text{-}4}$ (but not p_1) in other pinnipeds, and (3) the relative size, location, and occlusal pattern of the secondary teeth that succeed them also correspond to those of $P_{2\text{-}3\text{-}4}$, rather than of $P_{1\text{-}2\text{-}3}$. The supporting evidence for these criteria is discussed below in *Comparative Dental Formulae*.

The ontogeny of the primary dentition, as seen in my series of fetuses was as follows:

Fetus, 106 mm, 11 August (stained and cleared).—Shallow depressions in the alveolar bone of the upper and lower jaws indicated the presence of follicles of

$$i\frac{2\text{-}3}{3}\ c\frac{1}{1}\ p\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4} \times 2 = 24.$$

Some of these can be seen in Fig. 48 (left). The palate of this specimen was

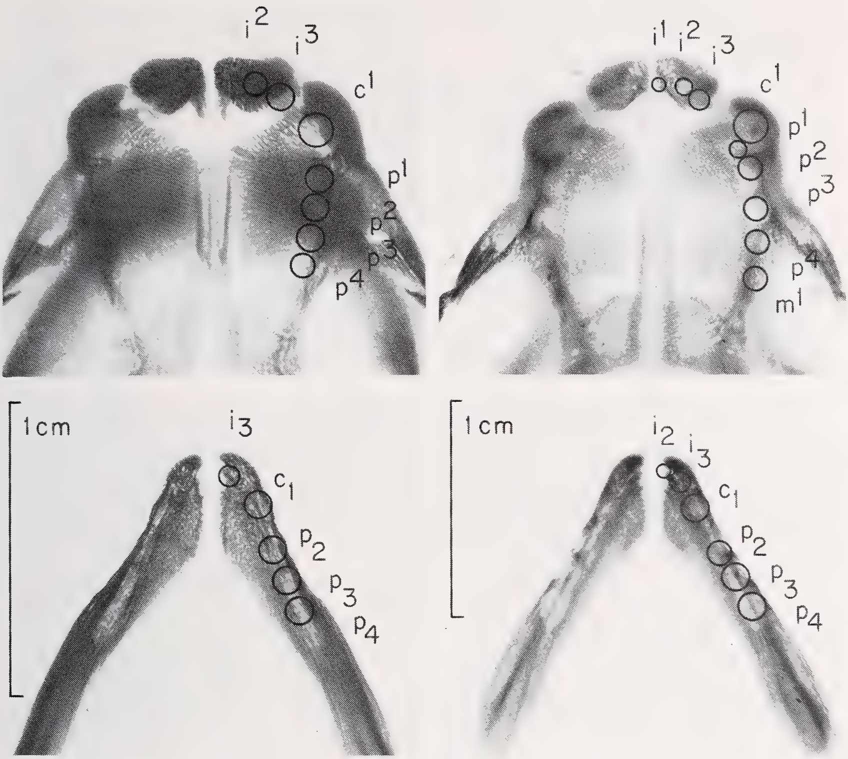

Fig. 48. Dental alveoli in stained and cleared skulls (upper-ventral view) and mandibles (lower-dorsal view) of 106-mm (left) and 132-mm (right) fetal walruses. (Photos by K. L. Austerman)

broader at the anterior than at the posterior end, such that the maxillary tooth rows were strongly divergent anteriorly. The upper canines were about twice as large as the premolars, with which they were aligned in the tooth row. In the lower jaw, distinct diastemata were present between i_3 and c_1, as well as between c_1 and p_2. No molars were evident, and none of the teeth had begun to calcify.

Fetus, 132 mm, 3 August (stained and cleared).—Primary follicle formula

$$i\,\frac{1\text{-}2\text{-}3}{2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{1}{\quad}\times 2 = 30.$$

The positions of most of the alveoli, as well as calcification centers in those of c^1 and p_3 can be seen in Fig. 48 (right). The alignment of the maxillary tooth rows was remarkably different from that in the previous specimen, due to broadening of the palate posteriorly. The upper canine was already outside the incisor-postcanine tooth row, in its characteristic position, lateral to p^1. The follicle of p^1 was smaller than those of the other premolars and no larger than it was in the previous specimen. The diastemata between the lower canine and i_3 and p_2 remained distinct but narrower than in the previous specimen.

Fetus, 178 mm, 18 August (L stained and cleared; R serially sectioned).—Primary follicle formula

$$i\,\frac{1\text{-}2\text{-}3}{1\text{-}2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{1}{1}\times 2 = 34.$$

Calcification centers were present in all follicles except those of i^1, i^2, p^1, and the molars. In the serial sections, primordia of all of the secondary teeth, except I_1, I_2, and P^1, were identified; that of the upper secondary canine already showed a well-differentiated enamel organ. The diastema between i_3 and c_1 was not apparent, but that between c_1 and p_2 was wide. Primordia of secondary molars were present; as in man and other mammals, however, these apparently do not develop beyond the state of undifferentiated laminae.

Fetus, 186 mm, 20 August (L stained and cleared; R serially sec-tioned).—Primary follicle formula

$$i\,\frac{1\text{-}2\text{-}3}{1\text{-}2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{}{1}\times 2 = 32.$$

Calcification centers were present in all but i^1, i^2, p^1, and m_1. The alveolus of i^2 in the left tooth row only was bisected by a slender ridge of bone, forming an elongate, double alveolus, as is often seen in the loci of the rudimentary secondary incisors of older specimens. The lower molars were not detected in the serially sectioned right half of the head, but the alveolus of m_1 was present in the stained and cleared left half.

Fetus, 208 mm, 10 September (stained and cleared).—Primary follicle formula

$$i\,\frac{2\text{-}3}{2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{1}{1}\times 2 = 30.$$

Calcification centers were present in all primary follicles except those of i^2, p^1, p^4, and the molars (Fig. 49, left). The alveolus of c^1 was more elliptical in cross section than in the younger specimens and extended farther posteriad. It was continuous with that of p^1 and separated from the alveolus of p^2 by only a slender ridge of bone. The follicle of i_2 was situated in a hemi-alveolus adjacent to the mandibular symphysis; that of i_3 was smaller and shallower than in any of the previous specimens. The diastema between c_1 and p_2 was still open on the right but closed on the left.

Fetus, 285 mm, 4 October (stained and cleared).—Primary follicle formula

$$i\,\frac{3}{1\text{-}2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{1}{1}\times 2 = 30.$$

Except for p^1, p^4, and the molars, each follicle contained the calcified crown of a tooth (Fig. 49, right). The follicle of p^1 was much smaller than those of the other premolars and was not appreciably larger than in the 106- and 132-mm specimens. The follicle of c^1 had attained the shape and alignment seen in older specimens. In the normal positions of i^1 and i^2 were several elongate slots in the alveolar bone, similar to those in the locus of i^2 in the 186-mm fetus. In the right lower tooth row, the follicle of i_3 was larger than that of c_1; on the left it was smaller than c_1. The latter seems to be the usual condition. The diastema between c_1 and p_2 was closed, bilaterally.

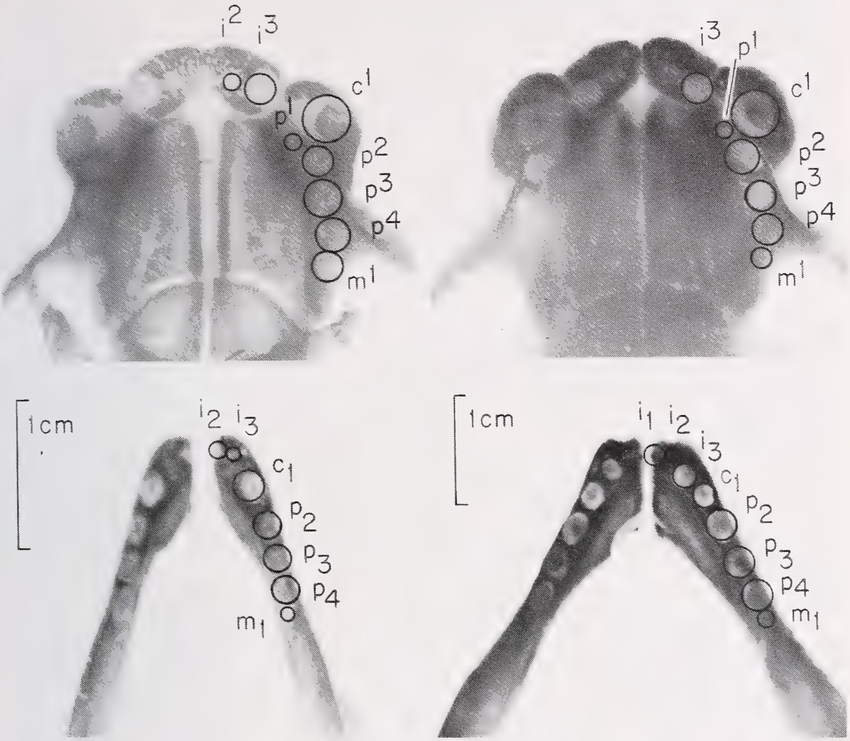

Fig. 49. Dental alveoli in stained and cleared skulls (upper-ventral view) and mandibles (lower-dorsal view) of 208-mm (left) and 285-mm (right) fetal walruses. (Photos by K. L. Austerman)

Fetus, 300 mm, 5 October (serially sectioned).—Primary follicle formula

$$i\,\frac{2\text{-}3}{2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{}{1}\times 2 = 28.$$

Unconsolidated dental laminae were present in the loci of i^1 and i_1 but were not sufficiently organized to be classed as follicles. There was no dental lamina in the locus of m^1. Whereas the follicles of i^2, p^1, and m_1 were incompletely organized and lacked any trace of calcified tissue, each of the other primary follicles was well organized and contained a calcified tooth. The diastema between c_1 and p_2 was closed, as it was in all older specimens. The secondary dentition was represented by follicles of

$$I\,\frac{1\text{-}2\text{-}3}{3}\;C\,\frac{1}{1}\;P\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}$$

and primordia of $M\,\frac{1}{1}$.

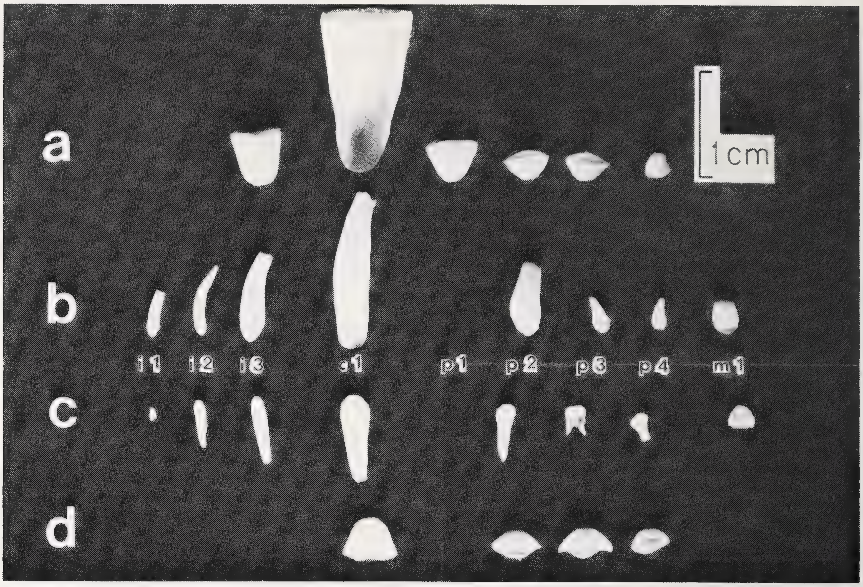

Fig. 50. Calcified teeth of a fetal Pacific walrus at 6 months post-implantation. Development of the primary teeth (rows b and c) is nearly complete, whereas only partial crowns of the secondary teeth (rows a and d) have developed. (Photo by G. C. Kelley)

Fetuses, 450–635 mm, 30 November–16 December. —Eight specimens were dissected and found to be about equally advanced in their dental development. None had the complete primary dentition, but one lacked only m^2 and m_2. The least number of primary follicles present was

$$i\,\frac{2\text{-}3}{2\text{-}3}\ c\,\frac{1}{1}\ p\,\frac{2\text{-}3\text{-}4}{2\text{-}3\text{-}4} \times 2 = 24.$$

The follicle of p^1 was identified in half of the specimens, but in only one of these was there any sign of its being calcified. The development of most of the other primary teeth had progressed to the extent that they had a well-formed crown and root (Fig. 50). The roots of p_3 and p_4 were bifid in some instances, and they and the other primary teeth more closely resembled those of otariids than of phocids (cf. Fig. 50 with Plate 11 of Scheffer and Kraus 1964). The crowns of the secondary teeth already were partly formed.

Full-term fetuses and newborn calves, 3–26 May. —The primary teeth of these specimens, examined by dissection, were in an advanced state of retrogression, commensurate with the rising secondary dentition, which was already well formed (Fig. 51). Only small remnants of the primary teeth remained, most of which were crowns alone, the roots having been resorbed. In the loci of most of the other primary teeth, only soft tissues or tiny caseous cysts about 1 mm in diameter remained. The minimal formula of calcified remnants was

$$i\,\frac{3}{}\ c\,\frac{1}{1}\ p\,\frac{2}{2\text{-}3}\ \ m\,\frac{}{1} \times 2 = 14;$$

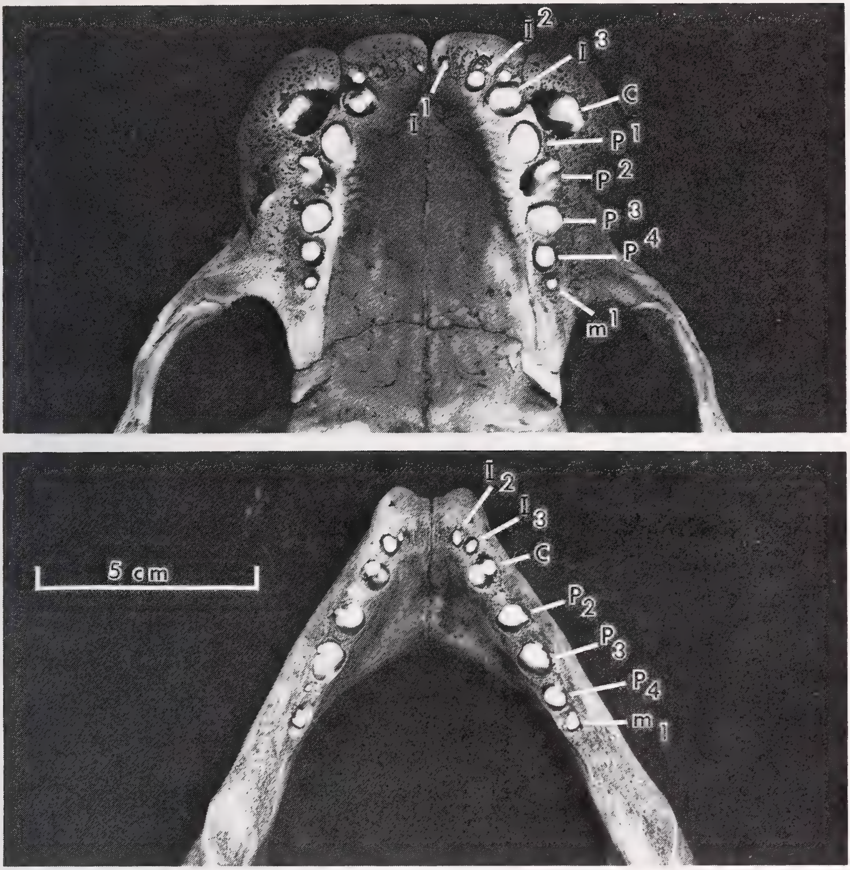

Fig. 51. Calcified dentition of a newborn Pacific walrus calf. Primary teeth present on one or both sides include $i^{2\text{-}3}$, c^1, $p^{2\text{-}3}$, and m^1 in the skull (upper-ventral view) and i_3, c_1, $p_{2\text{-}3\text{-}4}$, and m_1 in the mandible (lower-dorsal view); secondary teeth are as labelled. (Photo by K. L. Austerman)

the maximal formula was

$$i\,\frac{1\text{-}2\text{-}3}{2\text{-}3}\;c\,\frac{1}{1}\;p\,\frac{2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\;m\,\frac{1}{1}\times 2 = 30.$$

The follicle of p^1 was identified in less than half of these specimens; in no case was there any sign of its being calcified. Calcified tissue was absent in most cases also from the follicles of i^1, i^2, and the lower incisors. Even where there were no secondary successors, most of the primary incisors showed resorption of half or more of the tooth. Resorption seemed to have begun usually at the level of the cemento-enamel junction rather than on the apical part of the root. Partial resorption of the primary canines and premolars also was common, but it usually had begun on the lingual aspect of the root, adjacent to the secondary tooth.

The largest primary teeth, other than the molars, were i^3, p_2, p^2, and the upper and lower canines. Some of these also were gingivally erupted. In 28 calves examined only for gingival eruption of primary teeth, 9 had c_1 erupted, 3 had both c_1 and p_2 erupted, 1 had only p^2 erupted, and 15 had no erupted teeth. Gingival eruption of primary teeth usually constituted the merest penetration of the gingiva, to the extent that the tip of the crown was barely visible. None of the primary teeth was functional.

Older animals. — Most of my specimens that were more than 1 year old had no primary teeth other than the molars. Exceptions were a few 2-year-olds which retained one or two primary teeth, such as an upper incisor, an upper or lower canine, or p^2; one male that was more than 18 years old still bore both of its primary upper canines. Evidently, the molars usually are retained permanently, but they rarely become gingivally erupted and never occlude with an antagonist.

In summary, my findings indicate that most of the primary tooth germs already are well organized in the fetus within about 1.5 months post-implantation, and that calcification centers of all but the molars appear soon after, within the second month. Their development appears to be completed about 5 or 6 months post-implantation (about 5 to 6 months before birth), whereas full development of the molars is attained much later, about the time of birth.

Evidently, c^1 is displaced posterolaterad very early in this development, beginning in the second month. It reaches its ultimate position lateral to p^1 about 3 months post-implantation. Whether the postcanines migrate anteriad at the same time is not clear. In the lower tooth row, the displacement of c_1 posteriad into the normal position of p_1 seems to take place in cadence with the migration of the upper canine. This may be complemented by anteriad migration of the premolars, closing the diastema between c_1 and p_2 about 3 months post-implantation.

Each of the primary teeth is much smaller and more slender than its successor, is weakly rooted in a shallow depression in the alveolar bone, and has a simple crown and usually a single root. The primary teeth appear to reach their peak of development about the time when the secondary teeth begin to calcify. They are retrogressive at the time of birth and usually are resorbed in place rather than shed, whether or not they are succeeded by a secondary tooth. The frequency of their occurrence in the aggregate of my specimens was as shown in Table 9.

Secondary Teeth

The formula for the complete secondary dentition of the walrus is

$$\mathrm{I}\,\frac{1\text{-}2\text{-}3}{1\text{-}2\text{-}3}\;\mathrm{C}\,\frac{1}{1}\;\mathrm{P}\,\frac{1\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4}\times 2 = 30.$$

The secondary molars occur only as undifferentiated laminae in the embryonic dentition and do not to my knowledge ever attain the status of calcified teeth. None of my specimens possessed the full complement of calcified secondary teeth, but several fetuses had a full complement of secondary tooth germs.

Development of the secondary tooth germs begins at least as early as the second month post-implantation, and the tusk (C^1), seems to be the first to calcify. In the 178-mm fetus, the tip of the tusk was already partly calcified,

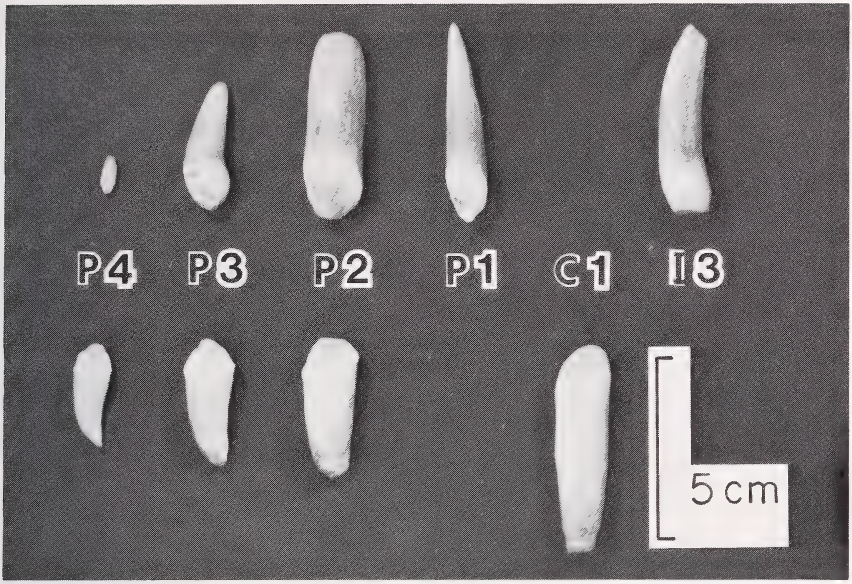

Fig. 52. Fully developed secondary teeth from a 4-year-old male Pacific walrus. (Photo by F. H. Fay)

whereas the laminae of the other secondary teeth had only begun to differentiate. In fetuses taken 4 months later, the tusks (still within the alveolus) were up to 15 mm long, in contrast to the 1- to 3-mm crowns of the other secondary teeth. In fetuses and calves taken during the perinatal months, the tusks were about four times longer than any of the other teeth.

The peak of development of the secondary dentition, in terms of maximal numbers of calcified teeth, seems to occur about the time of birth or somewhat earlier. Partial resorption of I^1, I_1, and I_2 often was detected at that time. Resorption of the vestigial secondary teeth evidently ceases during the first year after birth, and any subsequent losses of teeth are due to abrasion or shedding. Occasional losses of the larger, functional teeth also were recognized, and these seemed to be mostly due to periodontal disease or trauma. The postcanine teeth of old animals sometimes were shed when they became reduced to mere vestiges by continual abrasion. Two very old females had no teeth other than C^1.

All of the secondary teeth of the walrus have simple (haplodont) crowns and single roots (Fig. 52). The roots of the postcanines sometimes are longitudinally grooved, reminiscent of their former, double-rooted condition, as in the otariids. In general, they are longer and more robust than the primary teeth; only the rudimentary incisors may be no larger than their predecessors. The secondary incisors, other than I^3, sometimes remain unerupted for several years, but they usually are shed or resorbed within 2 or 3 years after birth. When gingivally erupted, they do not occlude with any antagonists.

The smallest of the secondary upper postcanines was P^4. This was one of the last to develop in the embryonic dentition and often was no larger than the first

Table 9. *Percent frequency of occurrence of primary teeth in relation to age.*[a]

Age in years from birth	No.	Upper										Lower								
		i1	i2	i3	c1	p1	p2	p3	p4	m1	m2	i1	i2	i3	c1	p2	p3	p4	m1	m2
−0.8 to −0.6	6	50	83	100	100	100	100	100	100	83	17	33	83	100	100	100	100	100	67	0
−0.4	8	62	100	100	100	50	100	100	100	100	0	25	100	100	100	100	100	100	75	12
0	13	23	31	100	100	0	100	15	38	85	0	0	31	31	100	85	61	69	77	0
2	11	9	0	18	9	0	0	0	0	64	0	0	0	0	0	0	0	0	73	0
3 to 10	12	0	0	0	0	0	0	0	0	58	8	0	0	0	0	0	0	0	50	17
11 to 30	17	0	0	0	6	0	0	0	0	41	6	0	0	0	0	0	0	0	41	6

[a] "Negative" ages are of fetuses, 9 to 7 and 5 months prepartum, respectively. In these specimens, each tooth was considered "present" if it was represented by an alveolus in the stained and cleared specimens or a tooth germ in the histological preparations. Only calcified teeth were counted in the remaining specimens (cleaned skulls), 0 to 30 years old. A tooth was scored as "present" in these specimens, even when it occurred unilaterally.

Table 10. *Percent frequency of occurrence of calcified secondary teeth in relation to age.*[a]

Age in years from birth	No.	Upper								Lower						
		I1	I2	I3	C1	P1	P2	P3	P4	I1	I2	I3	C1	P2	P3	P4
−0.4	4	0	100	100	100	100	100	100	25	0	0	0	100	100	100	100
0	14	43	79	100	100	100	100	100	57	7	21	71	100	100	100	100
1	15	20	87	100	100	100	100	100	47	7	20	47	100	100	100	100
2	11	9	91	100	100	100	100	100	36	0	0	54	100	100	100	100
3 to 10	12	0	42	100	100	100	100	92	50	0	0	8	100	100	100	100
11 to 30	17	0	6	100	100	100	100	100	41	0	0	6	100	100	100	94

[a] Negative age is of fetus 5 months prepartum. Unilateral, as well as bilateral occurrence, was scored as "present."

molar. It attained the status of a fully calcified tooth in less than half of my specimens, although it always was present in the fetal series as a well-differentiated tooth germ. Its calcification and eruption followed in sequence with the other secondary premolars. Whereas P^4 was gingivally erupted in about one-fourth of the 3- to 30-year-old specimens that I examined, it was only lightly abraded and never was large enough to occlude with an opposing tooth.

The frequency of occurrence of each of the secondary teeth in my specimens is shown in Table 10.

Ontogeny and Phylogeny of Canine Migration

Two unique characters of the walrus' dentition are: (1) reduction in size and posteromediad migration of C_1, and (2) radical enlargement and posterolaterad migration of C^1 to a position well outside the postcanine row. In my series of fetuses, both of these processes seemed to have been completed about 3 months post-implantation (about 8 months before birth), which implies that these are characters of long standing in the phylogeny of *Odobenus*. The fossil record seems to confirm that these changes took place long ago. The Miocene walrus *Aivukus cedrosensis* showed some enlargement of the upper canines, but both the upper and lower canines were in the "usual" canoid positions (Repenning and Tedford 1977). However, some greater advances toward the conditions in *Odobenus* were apparent in the early Pliocene walrus *Prorosmarus alleni*, which had large, somewhat laterally placed tusks, and its lower canines were reduced in size (Berry and Gregory 1906; C. E. Ray, personal communication). In the later Pliocene *Alachtherium*, the lower canine was greatly reduced in size and situated well back from the anterior end of the jaw; the upper canine had become a sizable tusk located lateral to the postcanine tooth row (DuBus 1867; Hasse 1909).

Comparative Dental Formulae

The problem of assigning practical descriptive notations to the highly variable dentitions of the walrus was addressed most recently by Cobb (1933), who devised a series of three formulae for the *deciduous*, *successional*, and *functional* teeth. These were intended to describe the typical dentitions of fetal, juvenile, and adult animals, respectively. Although that approach has some merit, it is not the conventional one for dyphyodont mammals. The customary notations are of formulae for the "deciduous" and "permanent" dentitions. The formula of the deciduous teeth comprises the primary incisors, canines, and premolars, which are shed at or soon after birth. The permanent teeth are the secondary incisors, canines, and premolars and the primary molars, which become the functional teeth of the adult.

By examination of serial histological preparations of the developing fetal dentition, I was able to determine that the primary dentition of the walrus includes tooth germs of at least three more pairs of teeth than were indicated by Cobb's (1933) findings from studies of prepared museum skulls. These additions were p^1, m^2, and m_2, none of which ordinarily is evident as a calcified tooth in cleaned skulls, though each did occasionally reach that stage of development in my series.

With these additions, the formula of the walrus' deciduous dentition, according to my findings, is

$$\mathrm{i}\,\frac{(1)\text{-}2\text{-}3}{(1)\text{-}2\text{-}3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{(1)\text{-}2\text{-}3\text{-}4}{2\text{-}3\text{-}4} \times 2 = 24 \text{ to } 30.$$

The teeth in parentheses were those found to be calcified in less than 50% of my specimens. The first upper and lower incisors and p^1 were the latest to develop and the least often calcified of any of the primary teeth, other than the molars.

In the secondary dentition, I identified four pairs of teeth in addition to those of Cobb's formulae: I^1 and the three lower incisors. Each of these also occurred infrequently as a calcified tooth but usually was present as a distinct tooth germ in the early developmental stages of the secondary dentition. By identification of p^1 and its successor, I confirmed that the first permanent upper premolar in the walrus, as in the northern fur seal (Kubota and Togawa 1970), is a tooth of the secondary, rather than primary, dentition.

The full comparative notation for the walrus' permanent dentition, with these additions, is as follows:

$$\mathrm{I}\,\frac{(1)\text{-}(2)\text{-}\ 3}{(1)\text{-}(2)\text{-}(3)}\;\mathrm{C}\,\frac{1}{1}\;\mathrm{P}\,\frac{1\text{-}2\text{-}3\text{-}(4)}{2\text{-}3\text{-}\ 4}\;\mathrm{m}\,\frac{(1)\text{-}(2)}{(1)\text{-}(2)} \times 2 = 18 \text{ to } 38.$$

The teeth in parentheses were present in less than 50% of my adult specimens. Thus, the walrus has the greatest potential number of teeth of any pinniped, but the least number occurring with greater than 50% probability. Even with the loss of P_1, the maximal formula of the walrus' permanent dentition is identical to that of many living canoid carnivores. Presumably, this large number of teeth is an atavistic character associated with the fissiped ancestry of the Otarioidea. Each of the other genera of pinnipeds has typically two or three pairs of deciduous and permanent incisors in the upper and one or two pairs in the lower tooth rows. Such reductions from the primitive state (from three pairs in each tooth row: Kellogg 1922) have been assumed to be due to loss of the first, rather than last incisors (see Scheffer and Kraus 1964). That assumption is upheld by my findings in the walrus.

In the upper tooth row of the walrus, there are four pairs of permanent premolars; in the lower row, three. Posterior to these in each row are one to two pairs of smaller teeth, usually situated somewhat out of alignment with the premolars. Cobb (1933) identified the latter as true molars (permanent teeth of the primary dentition), and I have confirmed that. The fifth and sixth postcanines in the upper row and the fourth and fifth in the lower row develop from tooth germs of the primary dentition. Lingual primordia of secondary successors occasionally are seen, but they apparently do not develop beyond that stage.

The four upper and three lower permanent premolars develop lingual to the follicles of their primary antecedents. Hence, they are of the secondary dentition. The first primary premolar (p^1) in the upper row ordinarily does not develop beyond the primordial stage, but $p^{2\text{-}3\text{-}4}$ go on to become well-formed, calcified teeth. The same pattern occurs in the northern fur seal (Kubota and Togawa 1970), in the harbor seal, *Phoca vitulina* (F. H. Fay and J. J. Burns, unpublished data), and presumably in all other pinnipeds.

Each of the three primary premolars in the lower tooth row develops labial to a permanent premolar and is a well-formed, calcified tooth. These teeth are similar to $p^{2\text{-}3\text{-}4}$ of the upper row and comparable to $p_{2\text{-}3\text{-}4}$ of the lower row in other pinnipeds (see Laws 1953*b*; Scheffer and Kraus 1964; Scheffer 1967*a*). The three secondary lower premolars of the walrus also resemble $P^{2\text{-}3\text{-}4}$ of the upper tooth row and are comparable to $P_{2\text{-}3\text{-}4}$ of the lower row in other pinnipeds, in that the first is about as large as or larger than the second and is at least as deeply rooted. This resemblance is indicated also by the occlusion of these teeth with the upper premolars. Whereas in all other pinnipeds and other carnivores, P_1 is situated slightly ahead of P^1, P_2 slightly ahead of P^2, etc., the first lower premolar of the walrus usually is situated behind P^1, the second behind P^2, and so on, in the "normal" occlusal positions of $P_{2\text{-}3\text{-}4}$ (see Cobb 1933, plates IV, V).

These findings pose the question of homologies of the three lower postcanines. Has the first or the fourth been lost from the primitive dental condition? Are the "survivors" $P_{1\text{-}2\text{-}3}$, as suggested for example by Berry and Gregory (1906) and Cobb (1933), or are they $P_{2\text{-}3\text{-}4}$? The available evidence suggests the latter. Although I found no traces of either a primary or secondary tooth germ of the missing first premolar in my fetal series, I suspect that these eventually will be identified, probably in fetuses younger than those available to me. In the meantime, I feel compelled to accept the circumstantial evidence, which indicates that the three lower premolars of *Odobenus* are 2-3-4, rather than 1-2-3. Absence of P_1 is not an unusual situation in carnivores (e.g., in many mustelids, some procyonids, hyaenids). Although its absence is unusual in pinnipeds, P_1 in other recent and fossil otarioids ordinarily is (or was) the smallest of the lower premolars (see Mitchell 1966, 1968; Barnes 1972; Repenning and Tedford 1977). In at least one of the modern forms, *Eumetopias jubatus*, P_1 is by far the smallest of the lower premolars and occasionally is absent from the tooth row (personal observation).

Two late fossil walruses believed to have been on the ancestral line to *Odobenus* had four well-developed lower premolars. The P_1 of *Aivukus cedrosensis* of the late Miocene North Pacific was slightly larger in diameter than P_2, but it was the less deeply rooted (Repenning and Tedford 1977). In the somewhat later *Prorosmarus alleni* of the early Pliocene North Atlantic, the P_1 was slightly smaller in diameter than the other postcanines (Berry and Gregory 1906) and, in my interpretation of a cast of the specimen (kindly provided by C. A. Repenning), it also was less deeply rooted than either P_2 or P_3. In *Alachtherium cretsii*, another fossil walrus of the Pliocene North Atlantic, four lower premolars also were present, the first of which was appreciably smaller than the second though still separated from C_1 by a wide diastema (DuBus 1867). In the cast of the mandible of *Prorosmarus*, P_2 is in precisely the same location as is the first lower premolar of *Odobenus*, relative to the mental foramen and coronoid process of the jaw.

Gingival Eruption of Secondary Teeth

The sequence of gingival eruption of the secondary teeth was determined in 60 free-living walruses, 0 to 6 years old, and in 3 captives when they were 2 to 15 months old. Data from the captives were provided by C. A. Hill (personal communication) of the San Diego Zoological Society. The order in which the teeth erupted through the gingiva and the ages (months) at which they first emerged were C_1 (2–4), C^1 (2–6), P_3 (3–8), I_3 (4–12), P_2 (8–12), I^3 (10–12), P^2 (11–13), P^3 (12–15), P_4 and P^1 (13–15), I^2 (14–15), P^4 (36–48). More than half of the teeth made their appearance in the first year after birth. By the end of the second year, the entire anatomical crown of each secondary tooth, except P^4, usually was gingivally erupted and occluded with its antagonist.

The percentage frequency of occurrence of gingivally erupted secondary teeth and primary molars in 136 specimens is shown in Table 11.

General Structure of Secondary Teeth

Each secondary tooth in the walrus calf at birth consists of a delicate, hollow cone of primary dentin capped with enamel and containing the dental pulp (Fig. 53*a*). The first thin layer of cementum is deposited on the exterior of the anatomical root, proximal to the enamel, in the second or third month after birth, well before most of the teeth have begun to erupt but about the time when gingival eruption of the canines begins. Development of the enamel cap on the anatomical crown of each tooth is completed at or soon after birth, before gingival eruption of the tooth. This cap, about 0.25 mm thick, is very fragile and is deleted by attrition and abrasion within a few years after eruption of the tooth. Usually, little or no enamel remains on any of the teeth, 6 or 7 years after gingival eruption.

Table 11. *Percent frequency of occurrence of gingivally erupted secondary teeth and primary molars in relation to age.*[a]

Age in years from birth	No.	I1	I2	I3	C1	P1	P2	P3	P4	m1
		Upper								
0	27	0	0	0	0	0	0	0	0	0
1 to 1.6	11	9	36	64	100	54	73	36	0	9
2 to 2.6	10	0	30	100	100	100	80	100	0	10
3 to 6	18	0	39	100	100	100	89	89	28	17
7 to 10	19	0	42	100	100	100	100	95	47	11
11 to 15	27	0	26	100	100	96	100	100	15	0
16 to 30	24	0	4	96	100	100	100	100	12	4
		Lower								
0	27	0	0	0	0		0	0	0	0
1 to 1.6	11	0	0	36	91		82	73	45	0
2 to 2.6	10	0	0	0	100		100	100	70	10
3 to 6	16	0	0	12	100		100	100	88	19
7 to 10	17	0	0	6	100		100	100	100	0
11 to 15	26	0	0	8	96		100	100	100	0
16 to 30	22	0	0	0	100		100	100	100	9

[a] Unilateral, as well as bilateral occurrence, was scored as "present."

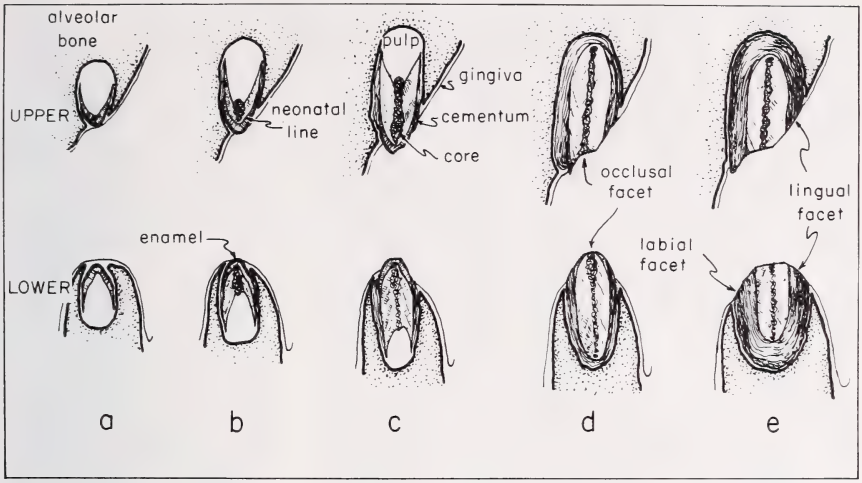

Fig. 53. Diagrammatic view of development and decrement of the walrus' first upper and lower permanent premolars. Transverse sections: (a) at birth, (b) at 1 year, (c) at 2 years, (d) at 7 years, and (e) at about 20 years of age.

Dentin

Deposition of dentin in the secondary teeth of the walrus takes place in two locations: on the walls of the pulp chamber and within the body of the pulp. The character of the dentin produced on the walls differs greatly from that deposited within the pulp. On the walls, it is laid down in smooth, opaque layers; within the pulp it is formed mainly as translucent, spherical globules, up to 0.5 mm in diameter. The globules are comparable in location and, apparently, in structure with the denticles or "pulp stones" in human teeth (cf. Johnson and Bevelander 1956). Whereas in man these are regarded as pathological and are associated with old age, they make up a major part of each normal tooth of the walrus from the first year. As these denticles gradually increase in size and number, they become interconnected by slender longitudinal strands of tubular dentin (orthodentin). Eventually, they coalesce or become amalgamated with further deposits of irregular tubular dentin (Fig. 54). This amalgam of denticles and irregular dentin constitutes the central "core" of each tooth, which is one of the most distinctive structural characters of the walrus' dentition (Penniman 1952; Cammann 1954; Ray 1975). In general, the core makes up about 40% of the volume of the tusks and up to 10% of the volume of the cheek teeth.

The core material contains an intricate network of vascular canals, mostly about 0.03 to 0.05 mm in diameter (Fig. 55). This network apparently is interconnected with vessels in the pulp. I have found traces of blood in these canals within a few millimeters of the pulp in the cheek teeth and up to 1 or 2 cm distal to the pulp in the tusks. In most of the cheek teeth and tusks that I examined in sagittal section, however, the more distal canals did not contain whole blood but a paler, more homogeneous fluid resembling plasma, serum, or lymph. This finding suggests that the canals usually are blocked by thrombi or

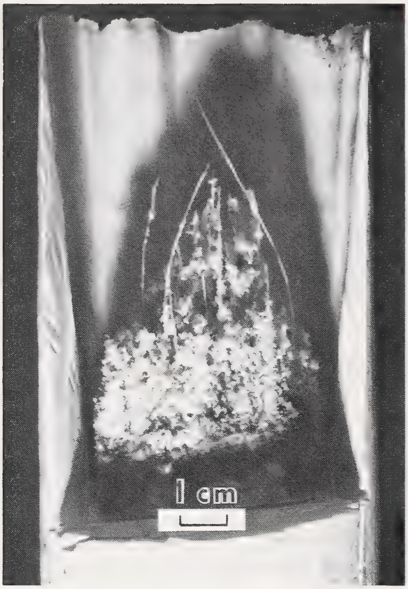

Fig. 54. Globular dentin in the pulp chamber of a walrus tusk from which the lateral wall has been sawed away. The pulp was removed by maceration. Slender vertical strands of tubular dentin (slightly distorted) interconnect the masses of spherical denticles. (Photo by G. C. Kelley)

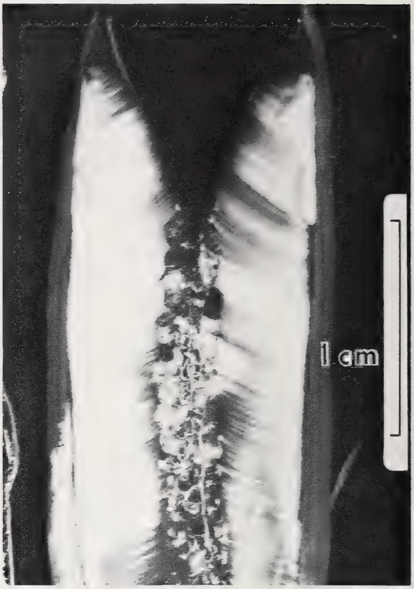

Fig. 55. Vascular canals in the central core of globular dentin. Partially cleared, longitudinal section from an upper premolar of a 3-year-old Pacific walrus. The central canals and radiating dentinal tubules appear whitish in this view under reflected light. (Photo by G. C. Kelley)

some other means of filtration, not far from the pulp. I determined that they are not completely blocked by filling the pulp chamber of a small tusk with carbon ink, excising the tip of the tusk to expose the core, and immersing the cut tip in a saline solution. The ink, drawn from the least to the greatest salinity, flowed for more than 3 cm through the core canals to the tip (Fig. 56).

I presume that the canals become permanently blocked by calcification in the more distal parts of the tusks, for I have seen no signs of blood, serum, or lymph oozing from the exposed (by natural abrasion) core of the tusks of normal, free-living adults. If these canals were not blocked, they would be avenues for disadvantageous loss of body fluids and ingress of pathogens. Walruses in captivity frequently abrade their tusks to an extreme degree, exposing the core to within a few centimeters of the pulp. In such instances, acute inflammation in the pulp from bacterial invasion is a common pathological condition (Brown 1963; Brown and Asper 1966; Bartsch and Frueh 1971; Ruempler 1976).

This central core of globular dentin apparently was absent from the teeth of *Aivukus cedrosensis* of the Pacific Miocene but appeared in the tusks of the earliest known walruses of the Atlantic Pliocene, which, by stratigraphic association, are believed to have been *Prorosmarus alleni* (Repenning and Tedford 1977; C. E. Ray, personal communication). Although lesser amounts of globular

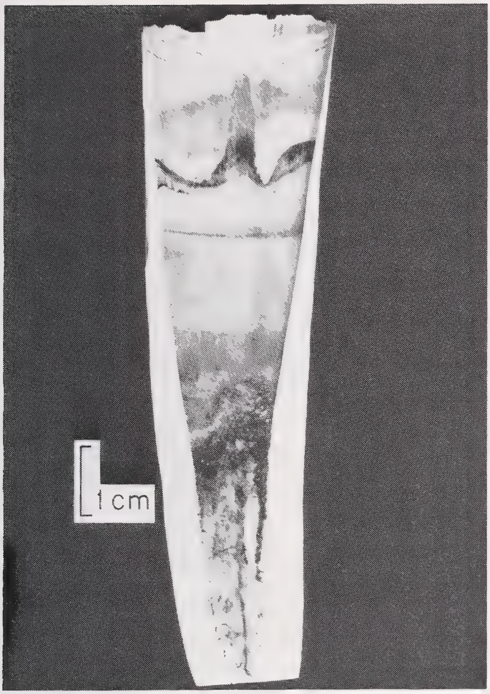

Fig. 56. Passage of carbon ink through the central canals in the tusk of a 2-year-old Pacific walrus. Direction of flow was from the pulp chamber (upper) toward the distal tip (lower), which was excised and immersed in saline solution. (Photo by G. C. Kelley)

dentin occur in the teeth and tusks of some other mammals (Ray 1975), in none that I have seen was the quantity at all comparable to that in *Odobenus.* Because of its vascularity, the globular dentin resembles to some extent (but is not homologous with) the vasodentin or osteodentin in the teeth of some lower vertebrates. The functional value of its vascular system is unknown, but the presence of a vascularized tusk in the narwhal (*Monodon monocerus*), the only other marine mammal with grossly comparable dental specialization, suggests some unifying adaptive purpose, possibly related to the marine environment.

The dentin deposited on the walls of the pulp chamber in teeth of *Odobenus* contains an abundance of fine tubules, in which are protoplasmic processes from the odontoblasts. The homologous processes in human teeth are believed to have a sensory, rather than circulatory function (Scott and Symons 1961). The tubules radiate outward from the central core of each tooth and appear to be interconnected to some degree with those in the core. The tortuous disarray of the tubules within the core identify this material as *irregular secondary dentin*, as distinguished from the *regular secondary dentin* deposited on the walls of the pulp chamber. In the regular secondary dentin, the tubules are only slightly sinuous and tend to be parallel.

The tubules in the regular secondary dentin appear somewhat S-shaped in longitudinally sectioned teeth. Slight secondary curvatures occur where the tubules are intersected by incremental "lines." These incremental lines are of two major types: those indicated only by secondary curvature of the dentinal tubules and those accentuated further by differential calcification. Lines of the first type appear to be products of two superimposed rhythms of dentin production, one at intervals of about 0.025 mm and the other at about 0.3 mm. Because of the regularity of these lines, they resemble the fine contour lines of rhythmic growth in the dentin of human teeth. The incremental lines of the second type, caused by differential calcification, are more irregular in quality and arrangement. I presume that they are correlated with general systemic disturbances, such as nutritional deficiencies and other physiological stresses of major importance (cf. Massler et al. 1941). The incremental lines that mark the beginning and end of each annual deposit of dentin are of this second type and are the most clearly expressed. The most prominent second type line is the "neonatal line," which (as in the teeth of other mammals) separates the dentin formed before birth from that formed after birth. Its homologue in man is believed to reflect an interruption of growth during the physiological stresses of the late prenatal and early postnatal period (Scott and Symons 1961:188). In the walrus, this interruption of growth is expressed also on the external surface of the teeth, where it appears as a slight depression just proximal to the anatomical crown (Fig. 53).

Dental Pulp

In the incisors, postcanines, and lower canines, the dental pulp initially is large, relative to the amount of calcified tissue, and the proximal end of the pulp chamber is very broad. The breadth of this opening (apical foramen) and the volume of pulp increase for 1 or 2 years after birth. Thereafter, the volume declines steadily in the cheek teeth, ending in closure of the apical foramen and complete filling of the pulp chamber by dentin (Fig. 53) usually in the fifth or sixth year after birth. All further accretionary growth of the cheek teeth is by addition of cementum alone, on the exterior of the root. Cementum is deposited over the apex of the root, after closure of the apical foramen. Even so, vascular connections are maintained between the dentin and the periapical tissues through minute, transcemental canals about 0.02 mm in diameter (Fig. 57). In the upper canines or tusks, the dental pulp does not diminish greatly in volume until old age, and the apical foramen remains wide open.

Cementum

The cementum of walruses is entirely of the "cellular" type, though there is some variation in quantity of cells or lacunae within and between layers. The least number of lacunae per unit of volume is found in the first layer (primary cementum), deposited soon after birth. Somewhat more are present in the dense, translucent layers that comprise the annual incremental lines; the greatest quantity is present in the opaque cementum between them.

The cementum deposited between the annual incremental lines in the teeth of immature walruses is mostly from 0.2 to 0.5 mm thick. Annual deposits in very old adults may be one-tenth as thick (Fig. 58). Each successive annual increment tends to be somewhat thinner than its predecessor (Mansfield 1958*a*).

The continual deposition on the root of each incisor, postcanine, and lower canine results in a cumulative increase in thickness of cementum with increasing age (Fig. 53). Since the annual layers tend to be successively thinner, the rate of increase in cumulative thickness declines with increasing age (Mansfield 1958*a*).

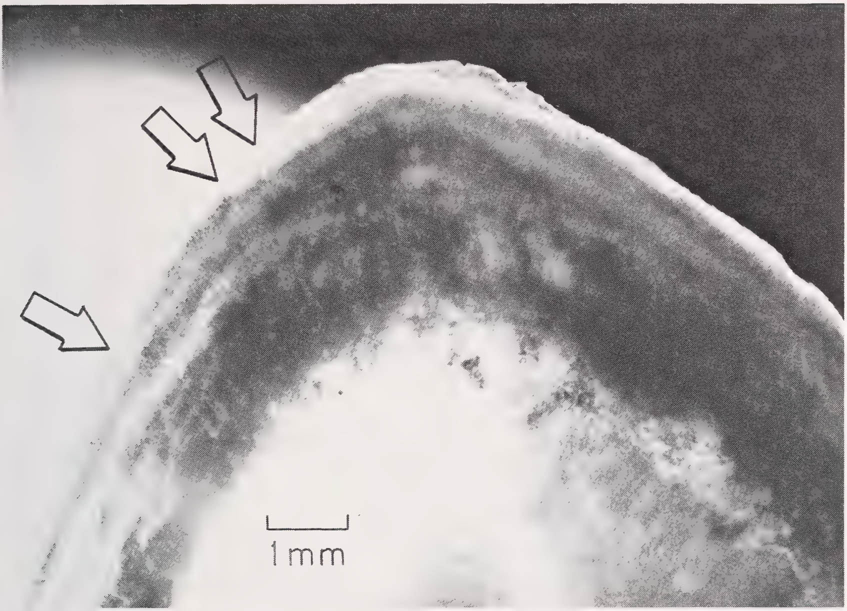

Fig. 57. Trans-cemental canals in the apex of the root of an upper permanent premolar of a Pacific walrus. Arrows point to three canals; others are evident near them. (Photo by G. C. Kelley)

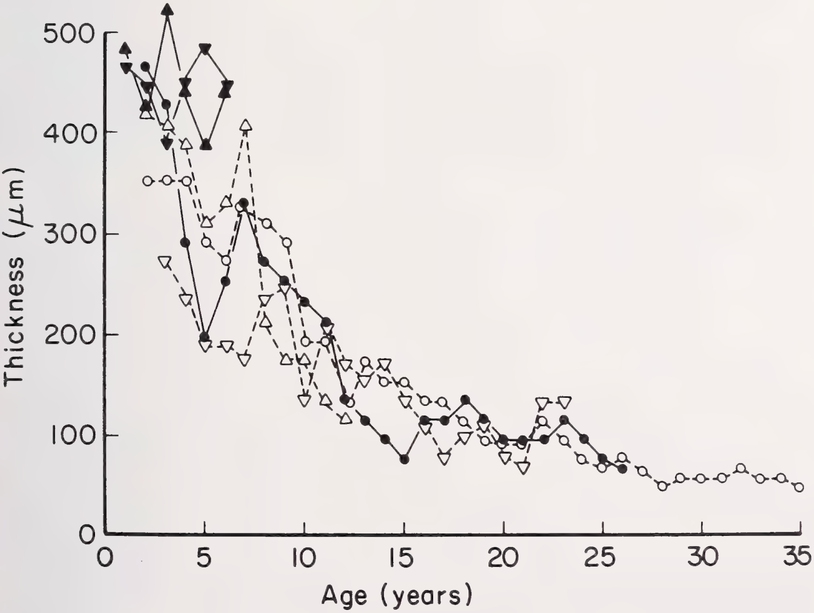

Fig. 58. Thickness of successive layers of cementum on the shaft of the root in post-canine teeth of some Pacific walruses. Each series of interconnected symbols represent data from one male (solid) or female (open).

However, even the thinnest annual layers are thicker than those on the teeth of most other mammals, and the total accumulation on the teeth of old walruses is, thus, exceptionally great. The maximum thickness of accumulated increments on the second upper premolar in two old males, 38 and 40 years old, was 10 and 11 mm, respectively. In those teeth, more than 90% of the total volume of calcified tissue was cementum.

Shape, Orientation, and Occlusion of Cheek Teeth

The dentition of the walrus, apart from the tusks, is made up of simple, peg-like (haplodont) teeth, of which only 16

$$(\mathrm{I}\,\frac{3}{-}\;\;\mathrm{C}\,\frac{-}{1}\;\;\mathrm{P}\,\frac{1\text{-}2\text{-}3}{2\text{-}3\text{-}4}\times 2)$$

are consistently present and functional. When fully developed, these are mostly 2.5 to 5.5 cm long and 1.0 to 2.5 cm in diameter. The most deeply rooted of these usually are I^3 and C_1; P^2 usually is the largest in diameter. These teeth range in cross-sectional outline from nearly round to slightly elliptical, the former being more typical of the upper and the latter more typical of the lower teeth. They taper to a blunt point at the proximal end (root apex), and the distal end (crown) ordinarily becomes obliquely beveled (upper teeth) or somewhat chisel-shaped (lower teeth) (Fig. 53).

The upper cheek teeth usually are somewhat longer than the lower, their combined lengths making up more than 50% of the total combined lengths of all of the teeth. This proportion increases with advancing age (Fig. 59), for all of the lower teeth tend to decrease in relative length, whereas some of the upper teeth increase (P^2, P^3), decrease (I^3), or remain stationary (Fig. 60). Evidently, I^3 has the highest rate of decrement of any of the teeth; P^2 has the lowest rate and becomes the longest tooth in the mouth. The rapid diminution of I^3, usually the most anterior tooth in the mouth, suggests that it has the greatest contact with abrasive materials.

The orientation and occlusion of the teeth were studied in some detail by Cobb (1933), mainly in skulls of adult males. He observed that the teeth are not set

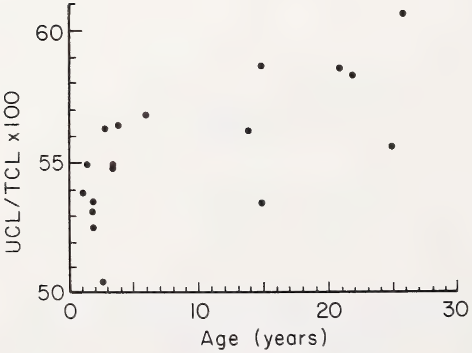

Fig. 59. Combined lengths of the upper cheek teeth (UCL), expressed as percentage of the total combined lengths (TCL) of all of the cheek teeth, in relation to age. Each point represents one specimen.

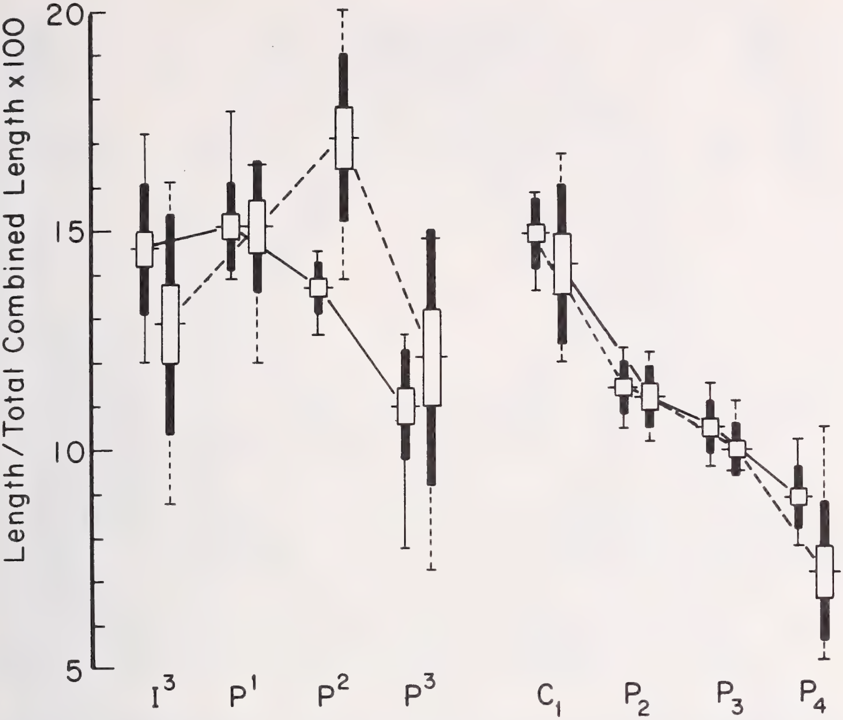

Fig. 60. Changes in relative length of the functional cheek teeth of the Pacific walrus with increasing age. Length of each tooth is expressed as percentage of the total combined length of all cheek teeth in one side of the mouth. Bars show range and mean ± 1 S.E. (open) and ± 1 S.D. (solid) of measurements from 11 animals 1 to 6 years old (connected by solid lines) and from 7 that were 14 to 26 years old (connected by dashed lines).

vertically in either the upper or lower toothrows but are mostly inclined anterolaterally some 10 to 20°; the upper teeth are more inclined than the lower (Figs. 61, 62). Many of the teeth also tend to be slightly arched (the lower more than the upper), with the anterior and lateral surfaces of the root concave and the posterior and medial surfaces convex. The lower canine usually is the straightest and most vertical; P^3 and P_4 are the most curved and obliquely set.

The occlusion of the cheek teeth with their antagonists resembles that in other mammals, in that the crowns of the upper teeth usually are slightly lateral to those of the lower teeth (Fig. 61, right). The occlusion differs most remarkably in the occlusion of I^3 exclusively with C_1, P^1 mainly with P_2, P^2 mainly with P_3, and P^3 almost exclusively with P_4. Although the lower teeth usually are situated somewhat posterior to their antagonists, the trend is toward end-to-end occlusion (Cobb 1933). In 30 specimens that I examined, 10 had nearly perfect end-to-end occlusion, 8 had end-to-end occlusion with the lower teeth slightly ahead (3) or slightly behind (5) the upper, and 12 had various combinations of end-to-end

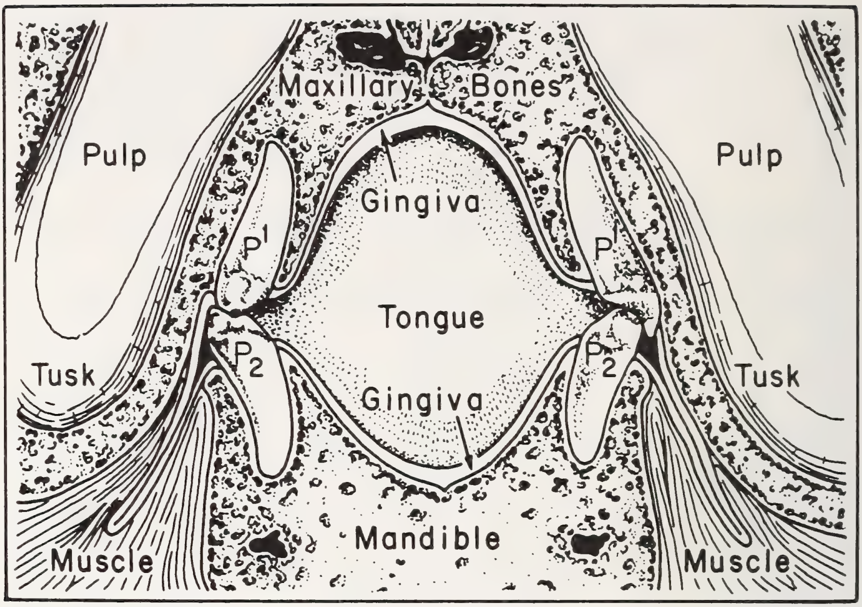

Fig. 61. Orientation and occlusion of the cheek teeth, as seen in transverse section of the mouth of an 11-year-old female at the anterior premolars. In most instances, the crown of the upper tooth is slightly lateral to its antagonist, as at right. (Adapted from photos by F. H. Fay)

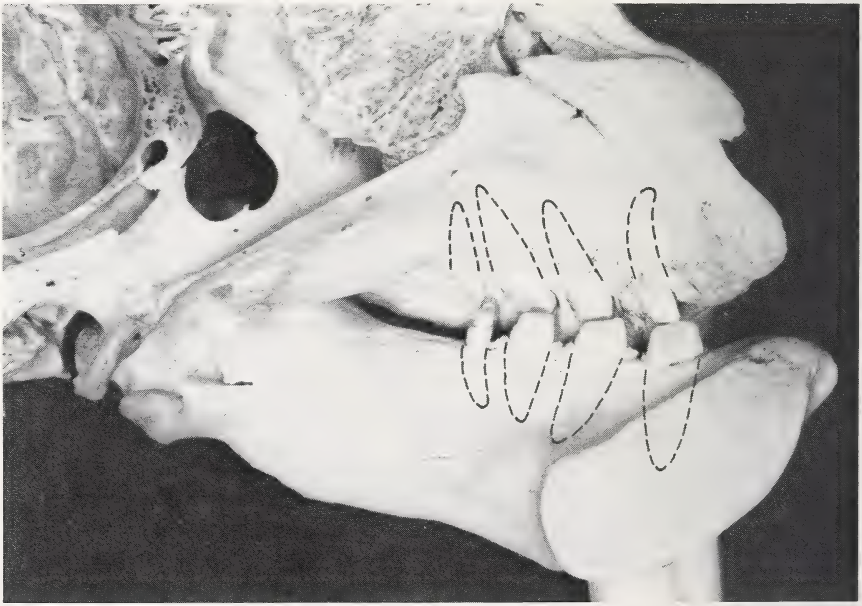

Fig. 62. Form and orientation of cheek teeth in the sagittal plane in a hemisected skull of an 11-year-old female. The approximate shape of the root of each tooth is indicated by dashed lines. (Photo by F. H. Fay)

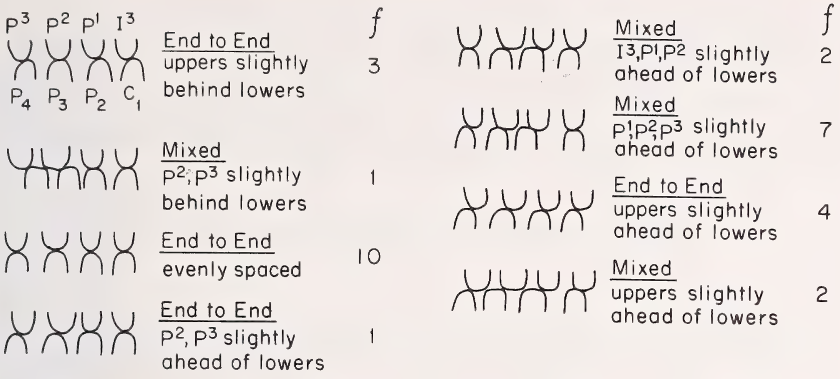
P^3 P^2 P^1 I^3
P_4 P_3 P_2 C_1
f
End to End
uppers slightly behind lowers
3
Mixed
P^2, P^3 slightly behind lowers
1
End to End
evenly spaced
10
End to End
P^2, P^3 slightly ahead of lowers
1
f
Mixed
I^3, P^1, P^2 slightly ahead of lowers
2
Mixed
P^1, P^2, P^3 slightly ahead of lowers
7
End to End
uppers slightly ahead of lowers
4
Mixed
uppers slightly ahead of lowers
2

Fig. 63. Frequency of occurrence (f) of eight occlusal patterns identified in the cheek teeth of Pacific walruses (10 males, 20 females).

and intermediate occlusion, in which the lower teeth tended to be ahead (1) or behind (11) the upper (Fig. 63). An extreme example of intermediate or "overlapping" occlusion, in which each lower tooth but P_4 (which was absent) occluded with two uppers, was illustrated by Cobb (1933: Plate IV). Cobb concluded that overlapping occlusion, because of its resemblance to that in other mammals, was more primitive than the end-to-end type.

The cheek teeth are incapable of chewing or grinding, other than by vertical action, for the mandible is hinged in such a way as to prevent side-to-side or forward-and-back motion. Furthermore, the mandibular symphysis, the "third joint" of the jaw (Scapino 1965), becomes solidly ankylosed at an early age. Thus, the occlusive stresses on the teeth are exclusively vertical-percussive.

Although the cheek teeth of the walrus generally have been regarded as "crushers," presumably for breaking the shells of clams, they differ greatly from the cheek teeth of other mammals in which crushing is known to be the primary or secondary function. First, the crowns are more or less conical and unicuspid; second, their protective enamel cap is extremely thin and fragile, and usually is lost entirely before the animal reaches adulthood; third, they lack a cingulum, which would provide added protection to the peridental gingiva from damage by the sharp edges of broken shells; and fourth, they all are single-rooted and mostly set obliquely, which would seem to be comparatively disadvantageous for absorbing the stresses of pounding and crushing.

With early loss of the protective enamel, each tooth is composed only of dentin and cementum, both of which are appreciably softer in the walrus than the same tissues are in the teeth of other carnivores. Since they also are softer than the shells of most of the mollusks that this animal consumes, one would expect the teeth to be worn down very rapidly if clam-crushing were a regular function. Yet the rate of decrement from the crown by attrition and abrasion is remarkably low, as is shown in the next section of this report. Furthermore, in the absence of a protective cingulum, one would expect the peridental gingiva and bone, especially about the premolars, to show either extensive damage or counteracting adaptive changes in structure, yet neither is evident. With the exception of I^3

and, especially C_1, the cheek teeth are not implanted in a way that seems adaptive to intense vertical pressure, and it is only on these and the more anterior vestigial incisors that intensive abrasion from large, hard objects seems to occur. Significantly, it is in that same area, on the incisive surfaces of the premaxillae and mandible, that the gingiva has become greatly modified to withstand the trauma of compression and other mechanical damage.

Growth, Attrition, and Abrasion of Cheek Teeth

Linear Growth

Linear growth of the cheek teeth is most rapid in the first 3 or 4 years after birth and practically ceases by the fifth or sixth year (Fig. 64). At that time, the deposition of dentin is essentially completed, even in the largest teeth (Fig. 53). With closure of the apical foramen, all subsequent increments of linear growth are by addition of cementum alone on the root apex. In the males, this apparently takes place on P^2 at a rate about equal to that of attrition from the crown, for the tooth does not change appreciably in length after closure of the apical foramen (Fig. 64). However, in the females, the rate of cementum increment on P^2 is slightly lower than that of coronal attrition, since the tooth becomes shorter with increasing age. In both sexes, the rate of increment on C_1 apparently is lower than the rate of attrition, for that tooth diminishes in length during the adult years at the rate of about 1 mm per year (Fig. 64).

The rate of linear increment by apical deposition of cementum on P^2 and C_1 is negatively correlated with age; at all ages, it tends to be greater on C_1 than on P^2 (Fig. 65). Although C_1 has the higher incremental rate, that tooth decreases in length with increasing age, whereas P^2, with the lower rate, remains more or less constant in length. As in I^3, this indicates that the rate of linear decrement from the crown is greater in C_1 than in P^2. That the decremental rates are not the same in all parts of the mouth is indicated also by measurements of actual amounts deleted from the crowns of C_1 and P^2 (Table 12). Although these rates did not differ between males and females, they did differ between teeth, that of C_1 being nearly twice as high as that of P^2.

Attrition and Abrasion

The removal of calcified tissue from the crown of each tooth takes place on four facets, only one of which is the product of occlusion (attrition) with the opposing tooth. That one, the *occlusal facet* (Fig. 66*a*, *b*), is clearly distinguished from the other three by its rough, pitted surface, usually concave on the upper teeth and convex on the lower. Ordinarily, it is rather small in area on the teeth of females (5 to 50% of the clinical crown) but rather large on the more robust teeth of the males (20 to 80% of the crown). The pits in its surface are mostly less than 0.5 mm in diameter and occasionally contain grains of sand and finer bottom sediments embedded in the dentin and cementum. I have found such particles common also in other parts of the mouth, as well as in the contents of the digestive tract, into which they apparently are taken in substantial quantities, along with the food (Fay et al. 1977).

The occlusal facet often is clearly delimited from the rest of the clinical crown

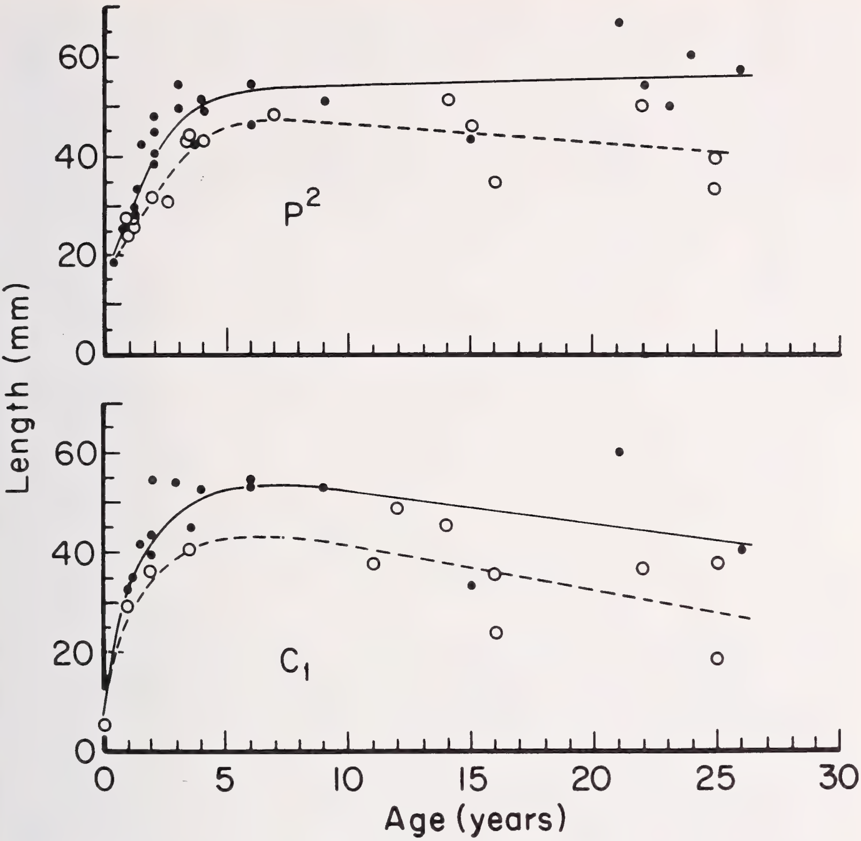

Fig. 64. Change in length of the second upper premolar and the lower canine with age in male (dots) and female (circles) Pacific walruses. Each point represents data from one specimen. Visually fitted curves are estimated means for males (solid) and females (dashed).

by a distinct ridge about its perimeter (Fig. 66*b*). This feature, and its remarkably perfect fit with the occlusal surface(s) of its antagonist(s), suggests that this facet is produced entirely by percussion of microlithic particles between the opposing teeth. The possibility that larger, hard objects, such as molluscan shells, are treated there seems remote, for mastication of those would tend to destroy the delimiting ridge and to blend the borders of this facet with those adjacent to it.

The second facet is the *lingual facet* which is located on the lingual (medial) surface of the clinical crown of each of the functional cheek teeth. This facet is oblique to the long axis of the tooth and, in adults, may be nearly parallel with the gingival surface (Fig. 66*b*). In middle-aged and older females, the lingual facet of the upper teeth often is on a level with the gingival surface (Fig. 67). This facet ordinarily is very large on the teeth of females, occupying 20 to 80% of the surface of the clinical crown; it is smaller on the teeth of males (5 to 60% of the

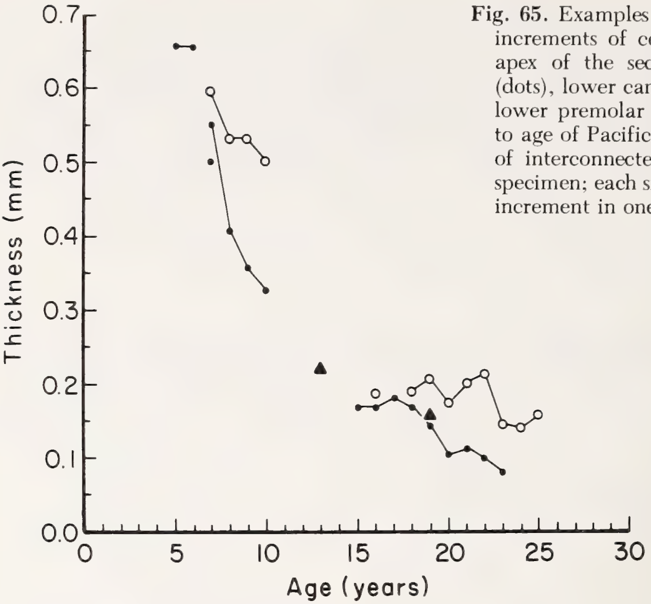

Fig. 65. Examples of thickness of linear increments of cementum on the root apex of the second upper premolar (dots), lower canine (circles), and first lower premolar (triangles) in relation to age of Pacific walruses. Each series of interconnected points is from one specimen; each single point is the latest increment in one specimen.

crown). Invariably, it is highly polished but typically shows also many fine striations made by abrasive particles. The orientation of those striae, almost without exception, is perpendicular to the principal (vertical) vector of occlusive force but is parallel to the long (horizontal) axis of the tongue. This orientation indicates that the abrasion of the lingual facet takes place mainly as a consequence of longitudinal motion of the tongue, carrying fine, microlithic particles. Vertical striations, such as one might expect to be inscribed by clam shells being crushed in this area, were conspicuously absent in nearly all of the approximately 50 specimens that I examined for this character.

The third area from which material is deleted from the clinical crown is the *labial facet.* This facet is present only on the mandibular teeth and is most apparent on P_2. Like the lingual facet, it always is highly polished and slightly

Table 12. *Estimated rates of linear decrement of dental tissue from the distal tip of the lower canine and second upper premolar of some Pacific walruses.*

	Specimens		Decrements		Estimated rates (mm/yr)	
Tooth	Sex	No.	Time (yr)[a]	Amount (mm)[b]	Range	Mean
C_1	M	3	22	35	0.89–2.50	1.59
	F	2	41	46	0.88–1.28	1.12
P^2	M	3	35	27	0.64–1.00	0.77
	F	4	48	33	0.62–1.00	0.69

[a] Sum of total years in which decrements took place.

[b] Sum of cumulative total measured amounts of decrement.

oblique to the long axis of the tooth. The striations made by abrasive particles on the surface of the labial facet rarely are as deep as those on the lingual facet; furthermore, they differ also in that they are inscribed vertically, parallel to the vector of occlusive force (Fig. 66*c*). The abrasion of this facet apparently takes place as a consequence of contact with the gingiva lateral to the upper cheek teeth and with that on the medial side of the base of the tusk (Figs. 61, 67). The labial facet occurs only in the presence of such contact and always is largest where that contact is greatest (on P_2). Very fine, microlithic particles, caught between the tooth and the gingiva, as the jaw is moved up and down, probably are responsible for all of the vertical striae. Tiny fragments of clam shells also could be involved, for the dentin and cementum are soft enough to be scored by such fragments. If the abrasion on this facet were entirely the result of clam shells being crushed in this area, a complementary facet should be produced on the medial–distal surface of the opposing tooth, when the occlusion is like that on the right side of Fig. 61. However, no such facet is produced; the medial surface of those distal flanges on P^1 and P^2, although nearly parallel to the lingual facets of P_2 and P_3, is highly polished and bears fine horizontal striae, perpendicular to those on the labial facets. Thus, the abrasion on the distal flanges is the same as that on the lingual facet (Fig. 66*b*).

The fourth type of abraded surface is the *incisive facet.* The abrasive process that produces this facet affects only the crowns of the vestigial incisors and, occasionally, the anteromedial surface of I^3 and C_1. The incisive facet is pitted, somewhat like the occlusal facet, from which it differs, however, in that (1) there is no occlusion with an opposing tooth, (2) the facet is not delimited by a peripheral ridge, (3) the edges of the pits are rounded, and (4) the surface between the pits is polished (Fig. 66*d*).

The incisive facet on the vestigial incisors occupies the entire clinical crown, which is worn down level with the gingiva (Fig. 66, inset). On those incisors, its surface is not only pitted but is deeply incised as well, the coarse striae being mainly parallel with the long axis of the oral cavity and tongue, as if made by coarse abrasives moving into and out of the mouth. Where this facet occurs on I^3 and on C_1, it may occupy up to 10% of the anteromedial surface of the crown. There, as on the vestigial incisors, it also has many coarse striae, but these range in orientation from oblique (60 to 70°) to parallel with the vertical vector of percussive force. On I^3 and C_1, the posteromedial border of the incisive facet often blends with the anteromedial border of the lingual facet, indicating that the rounding and polishing of its pits and striae are the result of lingual abrasion.

If any of these four types of abraded facets were the result of crushing and mastication of molluscan shells, as has been assumed previously (Cobb 1933), they should be absent from the teeth of walruses reared in captivity on a diet of fishes and shell-free clam meats. With this in mind, I examined the teeth of eight such specimens, ranging in age from 2.4 to 15.3 years and found the following:

- In all animals, the occlusal facets were similar to those on the teeth of free-living walruses.
- In the five oldest animals, the lingual facets were nearly the same as those of free-living walruses, except that they usually were not as highly polished, seldom showed any striae, and usually were not as intensively abraded. In the remaining three animals, the lingual facets were similar in shape to those on the teeth of

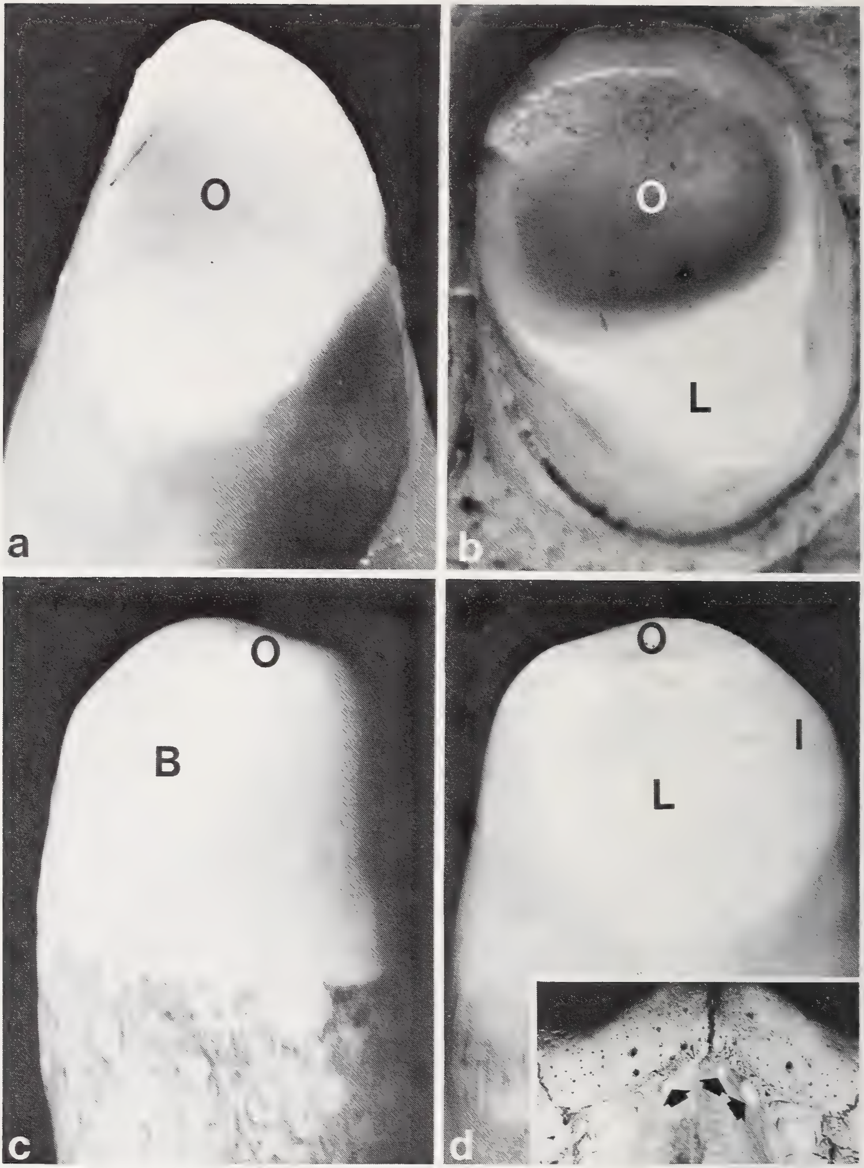

Fig. 66. Examples of the four types of abraded facets on the cheek teeth of Pacific walruses: (a) occlusal facet (O) on I^3, (b) occlusal and lingual (L) facets on P^2, (c) labial facet (B) on P_2, and (d) blending of the incisive facet (I) with the labial and occlusal facets on C_1. Inset, abrasion of the vestigial upper incisors (arrows) to the level of the gingival surface. (Photos by K. L. Austerman and G. C. Kelley)

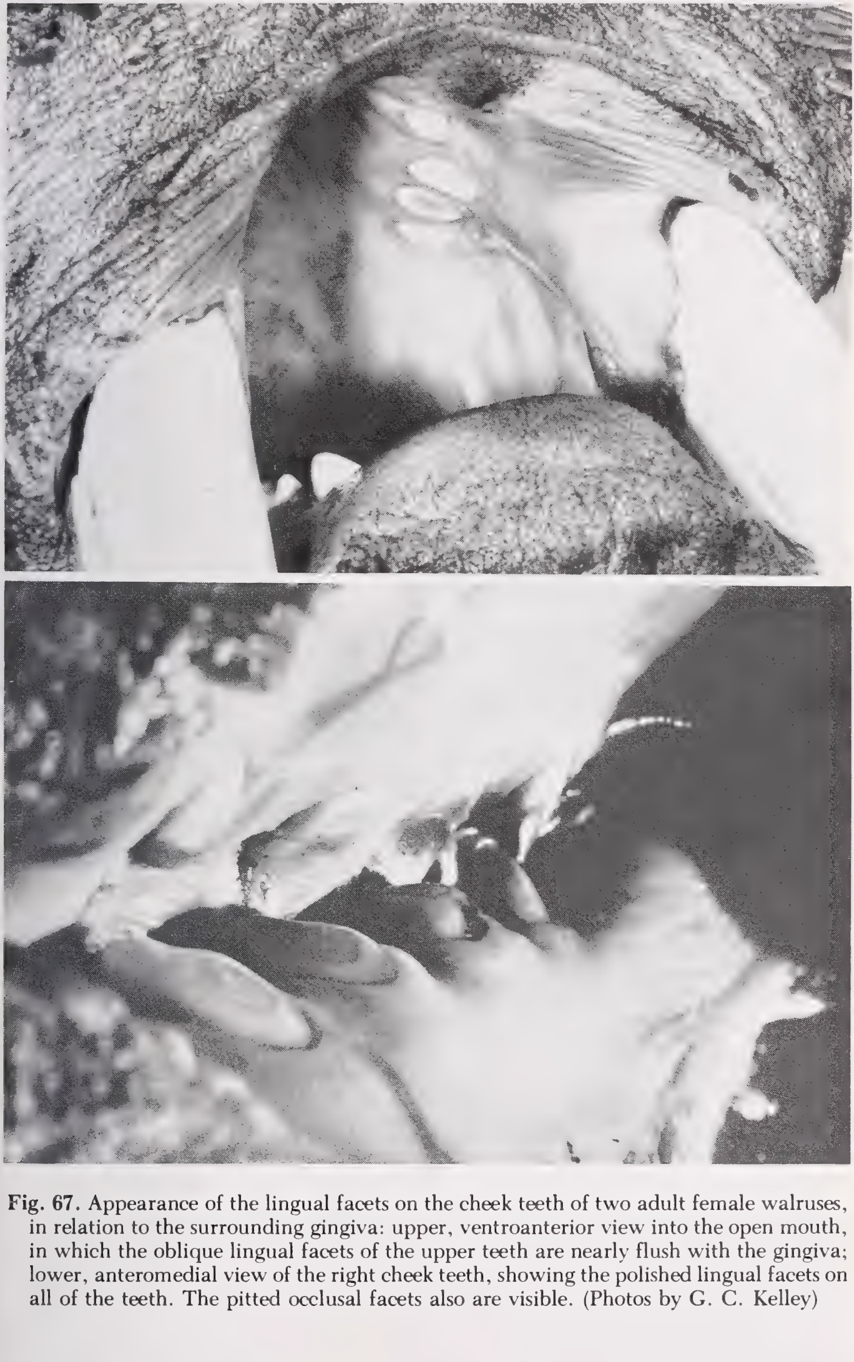

Fig. 67. Appearance of the lingual facets on the cheek teeth of two adult female walruses, in relation to the surrounding gingiva: upper, ventroanterior view into the open mouth, in which the oblique lingual facets of the upper teeth are nearly flush with the gingiva; lower, anteromedial view of the right cheek teeth, showing the polished lingual facets on all of the teeth. The pitted occlusal facets also are visible. (Photos by G. C. Kelley)

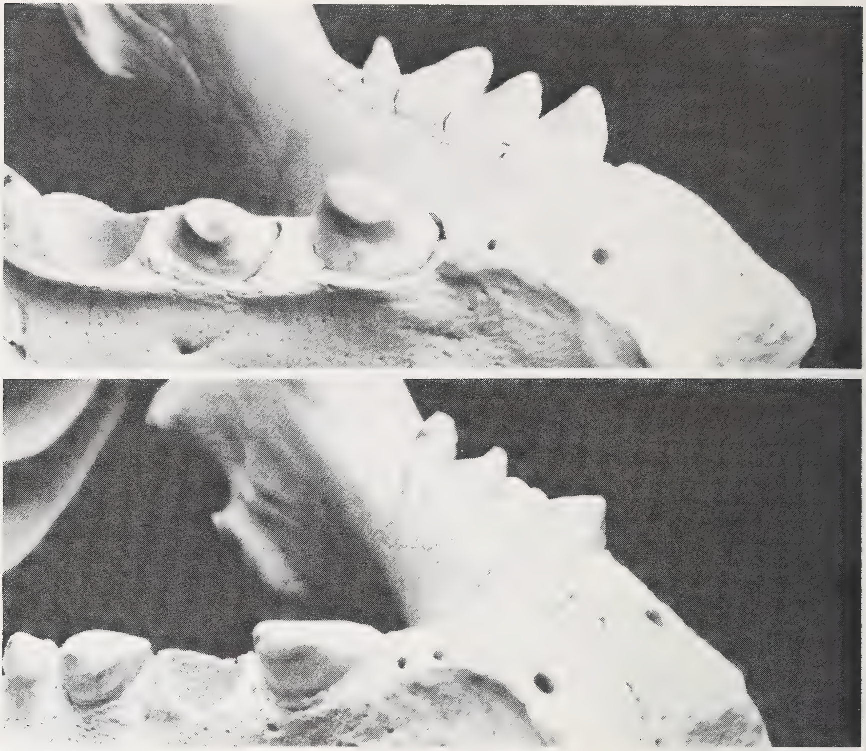

Fig. 68. Comparative views of the lower cheek teeth of captive and free-living Pacific walruses: upper, from a 7-year-old male reared in captivity at Marineland; lower, from an 11-year-old male taken in the Bering Sea. (Photos by G. C. Kelley)

free-living walruses, but they showed little or no sign of abrasion (Fig. 68).

- Small labial facets, comparable to those in many free-living walruses but lacking the polish and striae, were present wherever the lower teeth contacted the gingiva lateral to the upper tooth row.
- There were no incisive facets on any of the teeth.

In most of the captives, the crowns of all of the teeth were somewhat higher than those in free-living walruses and differed also in having significantly greater superficial calcareous deposits (tartar). The near absence of abrasives, whether clam shells or bottom sediments, would account for these differences as well as for the lack of polish and scarcity of incisions. However, in the absence of clam shells and with only small amounts of bottom sediments (in and among the clam meats), these captive animals had developed well-defined occlusal, lingual, and labial facets, closely resembling those in free-living walruses. The presence of these facets indicates that they are not produced exclusively by feeding on hard-shelled mollusks, although they are more clearly expressed in that situation. Conversely, the absence of incisive facets on the teeth of the captives indicates that these facets alone are produced by some items in the natural diet that were

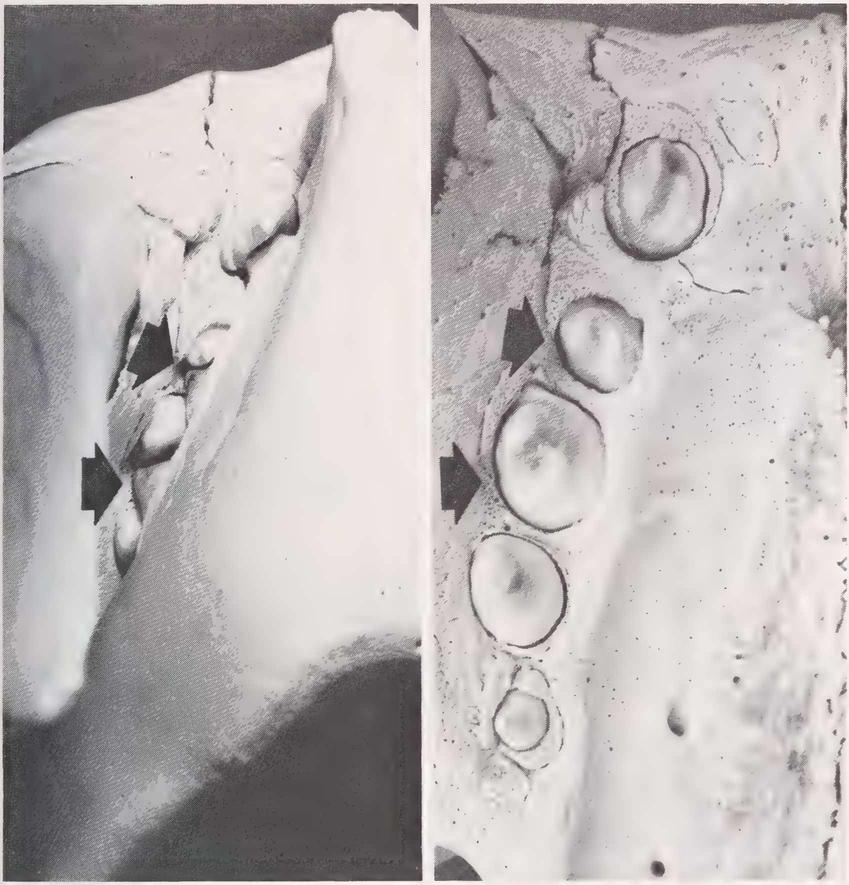

Fig. 69. Pressure-induced resorption of alveolar bone in a walrus reared in captivity on a shell-free diet of fishes and clam meats. Arrows indicate sites of occlusion of P_2 and P_3 with the maxillary gingiva adjacent to P^1 and P^2. Ventral views with mandible in place and teeth occluded (left) and with mandible removed (right). (Photos by G. C. Kelley)

not available to the animals reared in captivity, or by some feeding procedure that the captives did not or could not employ.

The skulls of several of the captives also showed the same kind of "basin-like excavations" in the alveolar bone, lateral to the upper teeth, which Cobb (1933:657) attributed to "pressure . . . by a hard substance in the food" (meaning clam shells). In these captives, as well as in the free-living walruses, I found that such depressions in the bone occurred only where the mandibular teeth occluded with the maxillary gingiva (Fig. 69). Although these basins are indeed sites of pressure-induced resorption and remodelling of the bone, the causative pressure appears to be from the teeth themselves, rather than from any intervening, hard substance.

Reduction in length of many teeth takes place also by resorption of tissue at the proximal end. This is a relatively minor cause of dental destruction, usually amounting to removal of no more than a millimeter or two of the cementum. As in man, such resorption takes place most often on the proximal third of the root and is found mainly in middle-aged or older individuals. The principal "exciting" causes of such resorption in human teeth are trauma and systemic disturbances, often associated with old age (Henry and Weinmann 1951).

As the crowns of the functional cheek teeth are worn away by attrition and abrasion, the teeth migrate distad, maintaining occlusal contact with their antagonists. Functional teeth that are unopposed, due to loss of an antagonist, also continue to migrate distad. These often develop a very high, polished crown that occludes eventually with the opposing gingiva. The vestigial incisors, P^4, and the molars, which are small, irregular in occurrence, and often unopposed, are more variable in their reactions to lack of an antagonist. The lower incisors and I^1 usually are resorbed in place, without ever becoming gingivally erupted. P^4 and the molars also seldom penetrate the gingiva. When they do erupt, they rarely extend beyond the level of full exposure of the anatomical crown. I^2 often becomes gingivally erupted, and continues to migrate distad until the tooth is completely destroyed by incisive abrasion.

Form, Development, and Abrasion of Tusks

The permanent upper canine teeth (C^1) of the walrus are recognized as "tusks" because of their great elongation, enlargement, and exposure. Their large size also identifies them as organs of great functional importance to the individual, hence of great adaptive significance for the evolutionary success of the species. In the past, the functional role of the tusks was more a subject for speculation than of definitive study. For at least 200 years, they were thought to function mainly in the acquisition of food, presumably being used as a digging or raking device for unearthing the clams. Recently, Miller (1975*a*, 1976) demonstrated that their major importance is as social organs.

Early in the present study, I observed that the supposed clam-digging function of the tusks did not seem to be upheld by the characteristics of their relative growth, abrasion, and placement in the skull. Hence, I devoted much effort to examining their structure and form and investigating their growth and abrasion. The objective of that work was to obtain indirect evidence of their function. The following are my findings.

Basic Form and Structure

At birth, the incipient tusks consist of simple, hollow cones of dentin, capped by enamel, and contained entirely within their alveoli (Fig. 70). At that time, each tusk is about 4 to 6 cm in overall length, the distal half of which comprises the anatomical crown. Gingival eruption of the tip of the crown begins during the first summer to autumn of extrauterine life; full gingival eruption of the anatomical crown is completed about 1 year later. In the 1-year-old walrus, the overall length of each tusk is more than double that in the neonate, and the enamel-covered portion exposed beyond the gingiva resembles the typical upper canine of a large carnivore (Fig. 71). Because this crown does not extend below

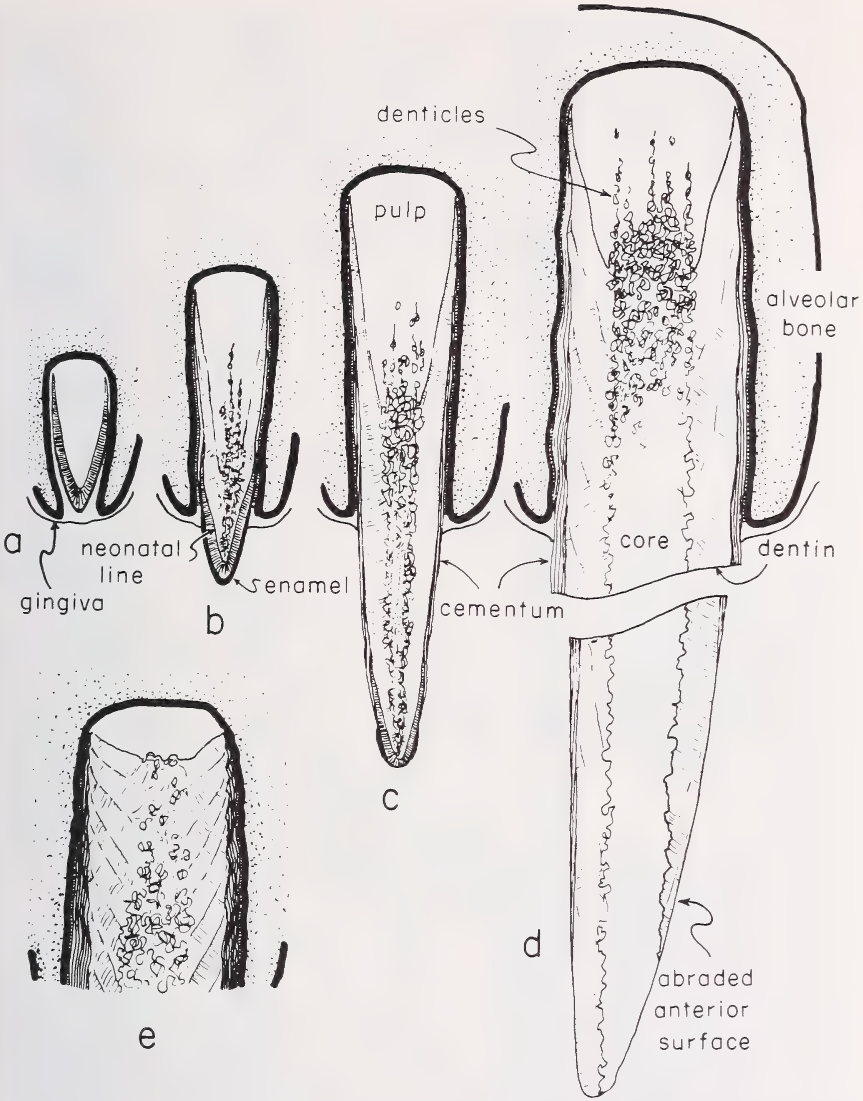

Fig. 70. Diagrammatic views of the development and internal structure of the walrus' tusks, as seen in longitudinal section: (a) newborn, (b) at 1 year, (c) at 3 years, (d) in adulthood, and (e) in old age.

the upper lip, it usually is not apparent in the living animal.

By 2 years of age, the tusks have increased in length to about 14 to 18 cm in females and 16 to 23 cm in males, about one-third to two-fifths of which is clinically erupted. By this age, the tip of the crown extends usually 2 to 4 cm below the edge of the upper lip and is beginning to show signs of discoloration

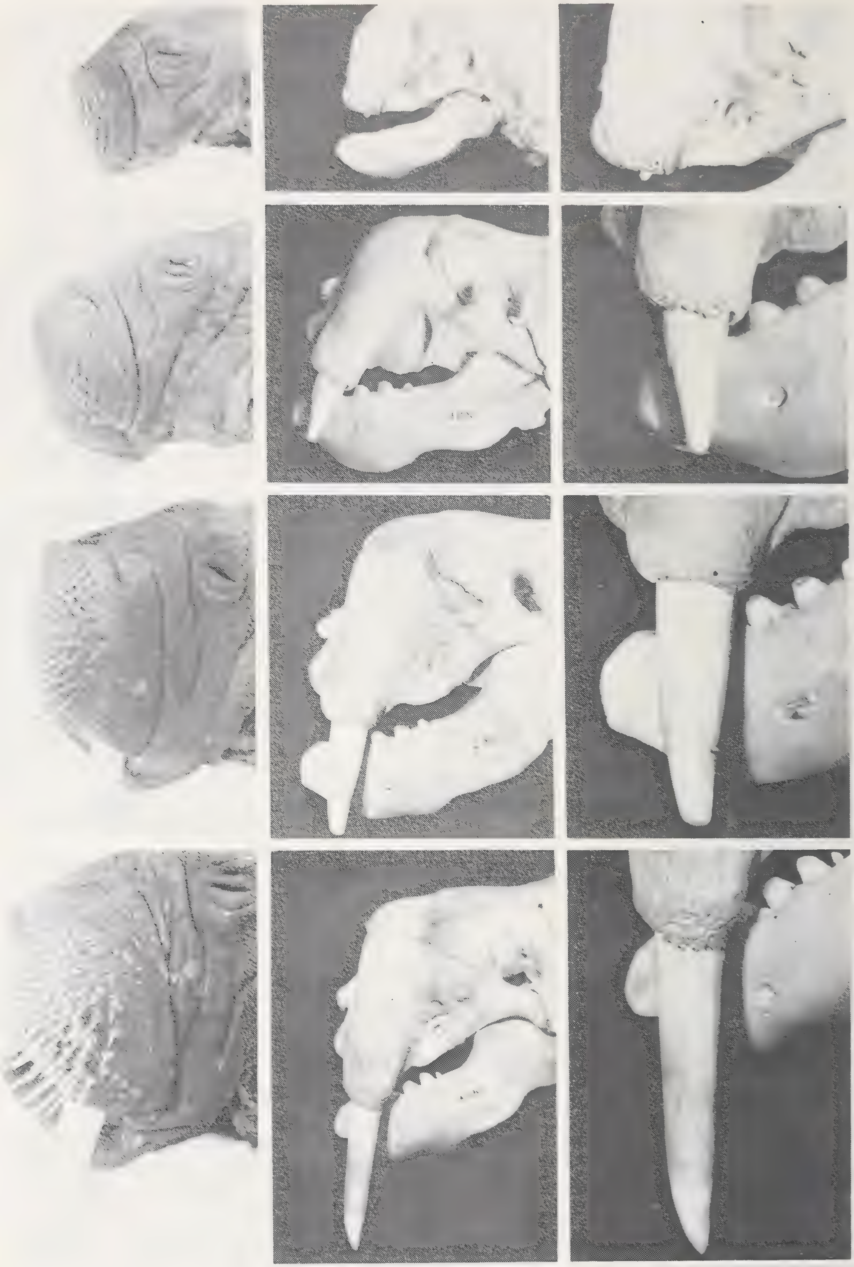

Fig. 71. Appearance of the tusks in free-living Pacific walruses at 0 (top), 1, 2, and 3 years of age (bottom): left, with facial flesh in place; center, in cleaned skulls; right, closeup views. (Photos by F. H. Fay and G. C. Kelley)

and abrasion. Though these tusks are hardly long enough to be used as digging or raking devices, it is at this age that most of the young become fully weaned and nutritionally independent of the mother.

By the end of the third year, about half of the tusk is clinically erupted, and more than half of the enamel has been removed from the anatomical crown by abrasion. Usually by the end of the fourth year, the enamel is absent or only a tiny plaque remains on the medial surface, near the tip of the tusk. From that time forward, the tusks are composed only of dentin and cementum. Eventually, the core of globular dentin becomes exposed near the tip, as the outer parts of the tusk are abraded away (Fig. 70).

In a longitudinal section of the tusk, one can see that each major increment of dentin takes the form of a hollow, truncated cone, in which the walls are thinnest proximally and thickest distally (Figs. 70, 72). Each conical increment of dentin that is formed in the pre-adult years is slightly larger in diameter proximally than its predecessor; those formed during adulthood are about equal in diameter. Each successive increment tends to be shallower than the preceding one, and the amount of globular dentin also tends to be less. In the tusks of very old animals, the latest increments are very thin and shallow and often lack the globular dentin. At that stage, the tusk is nearly solid to its base, and has only a thin, lenticular pulp at its proximal end.

That these major dentin increments are deposited on an annual basis was first suggested by Tomes (1904:195–196) and recently by Scheffer (1950) and Laws (1953*a*), who observed that the annular ridges on the root occur at regular intervals (Fig. 73). This regularity suggested that the ridges were formed by an annual rhythm of growth, like that in fur seals and elephant seals and that they might be counted for age determination. However, they usually are not apparent on the tusks of females or of immature males. Furthermore, on the tusks of adult males, the ridges usually are visible only on the proximal half or less of the root; more distally, they are obscured by overlying deposits of cementum. I confirmed that the ridges are produced annually by noting the position of the most proximal ridge, relative to the proximal end of the tusk, in animals taken in different months (Fig. 74). Apparently the ridge is formed in mid- to late winter, in the mating season, during temporary slowing or cessation of growth (cf. Kubota et al. 1961).

The pattern of deposition of cementum on the exterior of the tusks is rather different from that on the other teeth, in that all of the layers are of about the same thickness, and each overlaps only part of its predecessor (Figs. 70, 72). The proximal end of each annual layer of cementum is in contact with the proximal layer of dentin, formed in the same year. The distal end of each cementum layer overlaps one or more of the layers deposited in previous years. The extent of that overlap is inversely proportional to the rate of linear growth of the tusks, being least (about 60%) in the youngest animals, in which linear growth is most rapid, and greatest (more than 95%) in the oldest animals which have very slow growth. The cumulative thickness of cementum on the tusks is directly related to the extent of that overlap. Because of this, the greatest cumulative thickness of cementum in all tusks always is at or near the gingival margin (Figs. 70, 72). The thickness of cementum at that location in tusks of middle-aged males is about 2 to 2.5 mm; in very old males it may attain about 4 mm. In females, both the

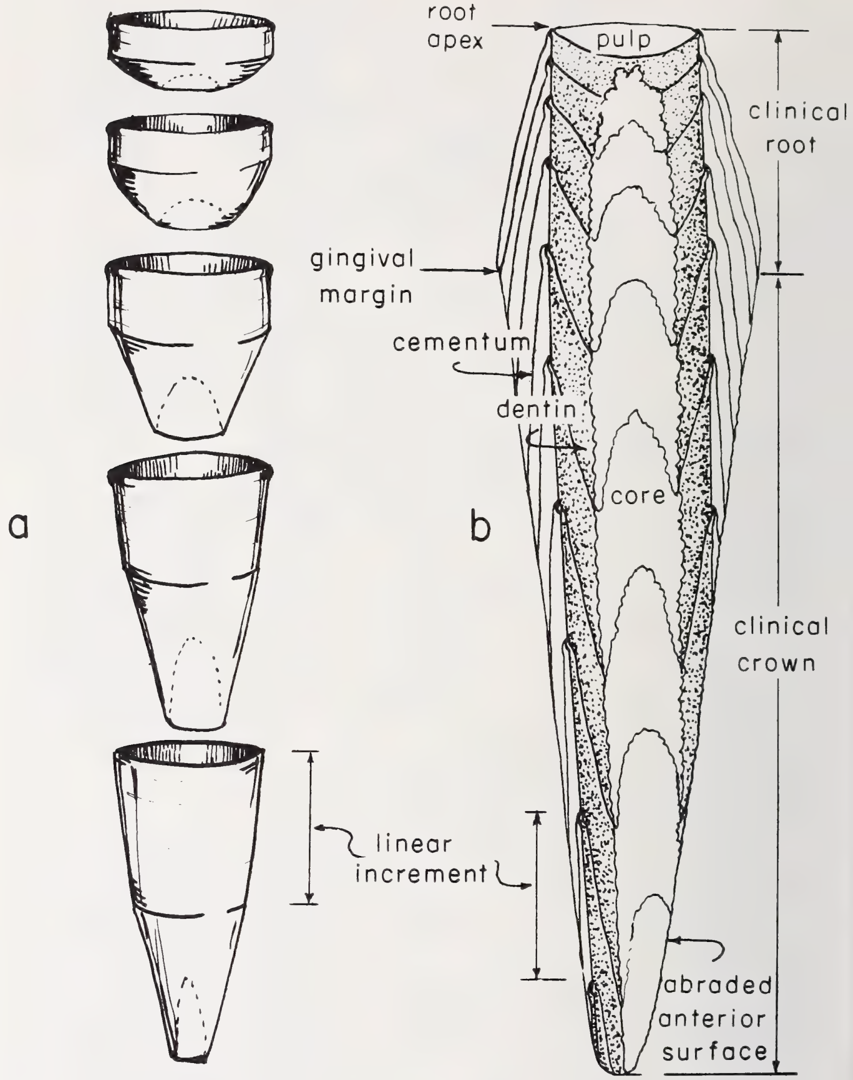

Fig. 72. Diagrammatic views of incremental growth of walrus tusks: (a) annual increments of dentin from youth (bottom) to old age (top), as they would appear if separated from the rest of the tusk; and (b) relation of dentinal and cemental increments as seen in longitudinal section.

individual layers and the total accumulation of cementum tend to be about two-thirds to three-fourths as great as those in males of comparable age.

Relation of Hypercementosis to Tusk Development

All of the walrus' teeth other than the tusks show hypercementosis. This is true

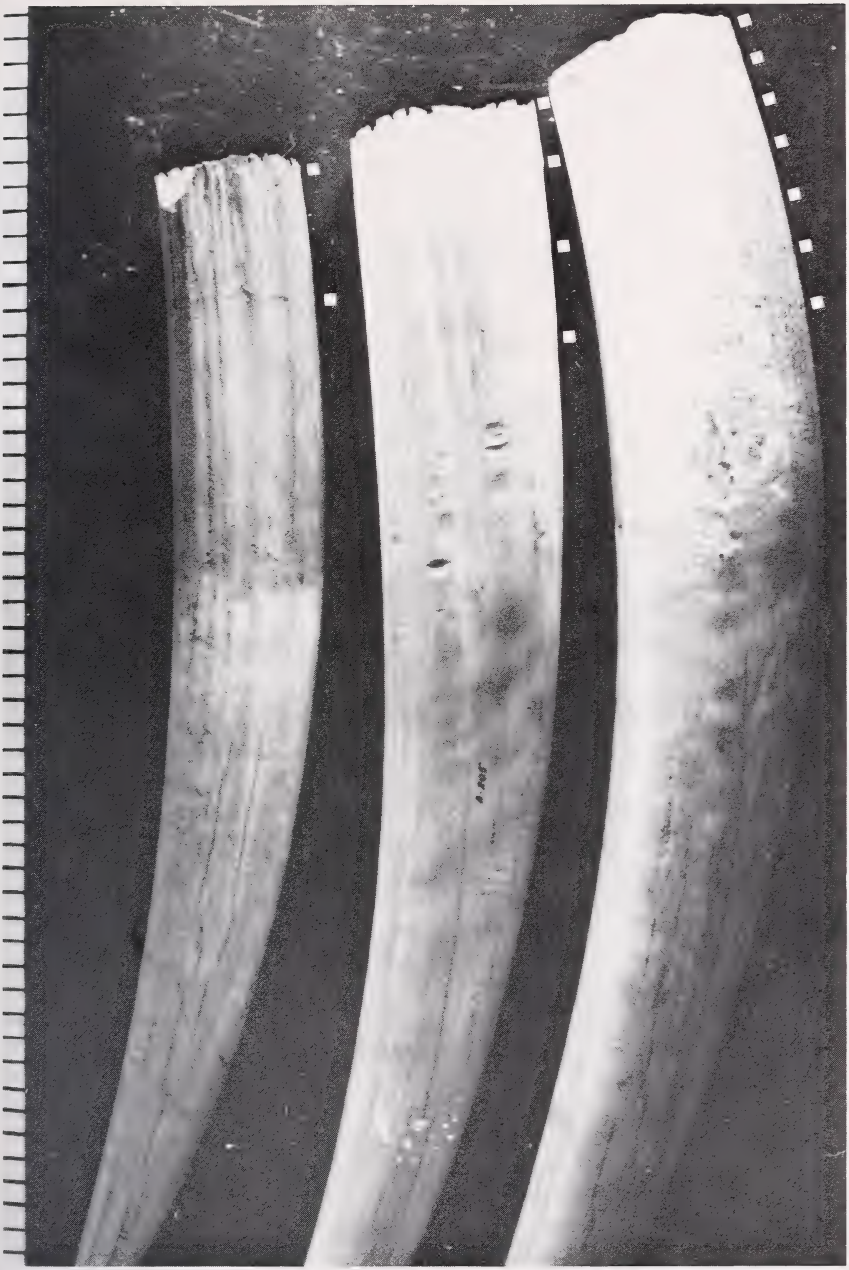

Fig. 73. Annular ridges on the roots of tusks from free-living Pacific walruses. White dots indicate position of each ridge on tusks of three males about 7 (left), 10 (center), and 25 (right) years old. Scale is centimeters. (Photo by F. H. Fay)

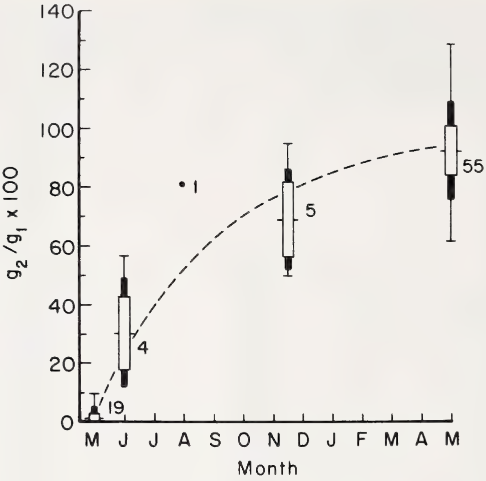

Fig. 74. Development of annual length increments in tusks of male Pacific walruses. Linear growth completed (g_2) in each month is expressed as percentage of the total increment in the previous year (g_1). Bars indicate range and mean ± 2 S.E. (open) and ± 1 S.D. (solid) for each monthly sample; numerals are sample sizes. Curve is estimated mean, based on assumed asymptote of 100%.

even of teeth that are not gingivally erupted. The deposition of cementum on all of the teeth commences in the first summer after birth, about the time when the tusks first penetrate the gingiva but well before any of the other teeth have begun to emerge. On the tusks, each increment of cementum is about as thick as its predecessor, but on the cheek teeth, the second year's increment usually is thicker than the first, the third is about as thick as the second, and the fourth and all subsequent increments are thinner than their precedessors. Those formed on the cheek teeth in the first 8 to 10 years usually are about twice as thick as those formed in the next 10; those in turn are much thicker and less clearly delineated than the layers formed in old age. These differences in thickness of increments suggest either changes in dental function or changes in an intrinsic physiological rhythm affecting cementum deposition.

Cementum serves primarily to attach the tooth in its socket by embedding the dental ends of the periodontal fibers, the opposite ends of which are anchored in the alveolar bone. When the tooth shifts in position, as in eruption or in response to changing stresses, the old fibers are replaced and more cementum is added for renewed attachment. While the teeth continue to function, cementum is continually added in response to such changes (Kronfeld 1938; Scott and Symons 1961). In man, who has an annual cycle of growth (Tanner 1962) but no other outstanding annual physiological or dietary cycles, the cementum tends to increase in thickness at a more or less constant rate (Zander and Hürzeler 1958). That is, the annual deposits are about equal in thickness.

In walruses, cementum is deposited on the teeth in an annual cycle, but only on the tusks are the annual layers equal in thickness. Those on the other teeth are unequal, and their variation in thickness does not appear to be correlated with any known characteristics of their function or development. The closest relation of the thickness of layers on the cheek teeth seems to be with the changing annual rates of linear growth of the tusks. Of all of the teeth, the tusks have the greatest need for continual renewal of periodontal attachment, because of their rapid growth and distad migration. Although the cementum increments on the tusks are all of about the same thickness, they are not all of the same volume, for those formed during years of rapid linear growth cover a much larger surface area than any formed in years of slower growth. The rate of linear growth of the tusks (hence, volume of cementum deposited) increases in the first 2 years, then decreases in essentially three stages thereafter. I suspect that this is the key to the rate of deposition of cementum on all of the other teeth. That is, the changes in relative volume of cementum deposited on each of the cheek teeth appear to be very similar to the changes in volume deposited on the tusks, where functional need for perpetually renewed attachment is most evident. Hypercementosis has been a consistent feature of the cheek teeth of odobenids only since the tusks began to enlarge beyond the usual canoid condition (Repenning and Tedford 1977).

Orientation and Shape of Tusks

The tusks are deeply rooted in the anterior part of the maxillae and extend downward from the corners of the mouth, on each side of the mandible. Their orientation, relative to the horizontal plane of the skull, is not perpendicular; they usually jut laterad and anteriad to some extent, rather than extending straight downward (Fig. 75*a*, *b*). For example, in 27 adults the roots of the tusks were inclined toward the midline of the skull at angles of 1 to 16° from the sagittal plane (mean, 8.1°) and were inclined posteriad 9 to 20° (mean, 13.8°) from the transverse plane. In each of these variables, there tended to be slightly greater variation among males than among females, but the means for each sex were comparable.

Each tusk is more or less elliptical in cross section, usually with one shallow longitudinal groove in the lingual (medial) surface and two in the labial (lateral) surface. The long axis of the ellipse generally is oriented antero-posteriorly but usually at an angle of 25 to 30°, rather than parallel to the midline (Fig. 75c). In 13 specimens, this angle ranged from 0 to 38° (mean, 28°), and the variation was about the same in both sexes.

Nearly all of the tusks that I examined had a slightly helical form, the right canine with a dextral spiral and the left, sinistral (Fig. 75*d*). The tusks of males generally showed the least tendency to spiral. In nine males, the amount of spiral per 50 cm of length ranged from none to 1/4-turn (0 to 90°), with a mean of about 1/16-turn (22°); in 11 females, the range per 50 cm was from none to 1/2-turn (0 to 180°), with a mean of 1/10-turn (36°).

The tusks are arched in the parasagittal plane, usually more so in females than in males (Fig. 76, upper). I measured the radius of this arc on the posterior surface of the tusks, using photographs of the lateral view of 30 skulls having the tusks in place. Radii in 18 males ranged from 45.6 cm to more than 5 m (mean, >150 cm); radii in 12 females were from 22.6 to 142.5 cm (mean, 72 cm). Expressed as a ratio of condylobasal length to radius of arc, the means for these males and females were about 1:3.2 and 1:1.9, respectively.

The tusks tend to be arched also in the paratransverse plane, though much less than in the parasagittal plane. In frontal view, this slight paratransverse arc, together with the helical form and parasagittal curvature, leads to the tendency for distal convergence of the tips in most females (Fig. 76, lower). Because of lesser helix and curvature in the males, their tusks tend to diverge. In the absence of fractures, the tusks of many females that are 20 years old or older often are

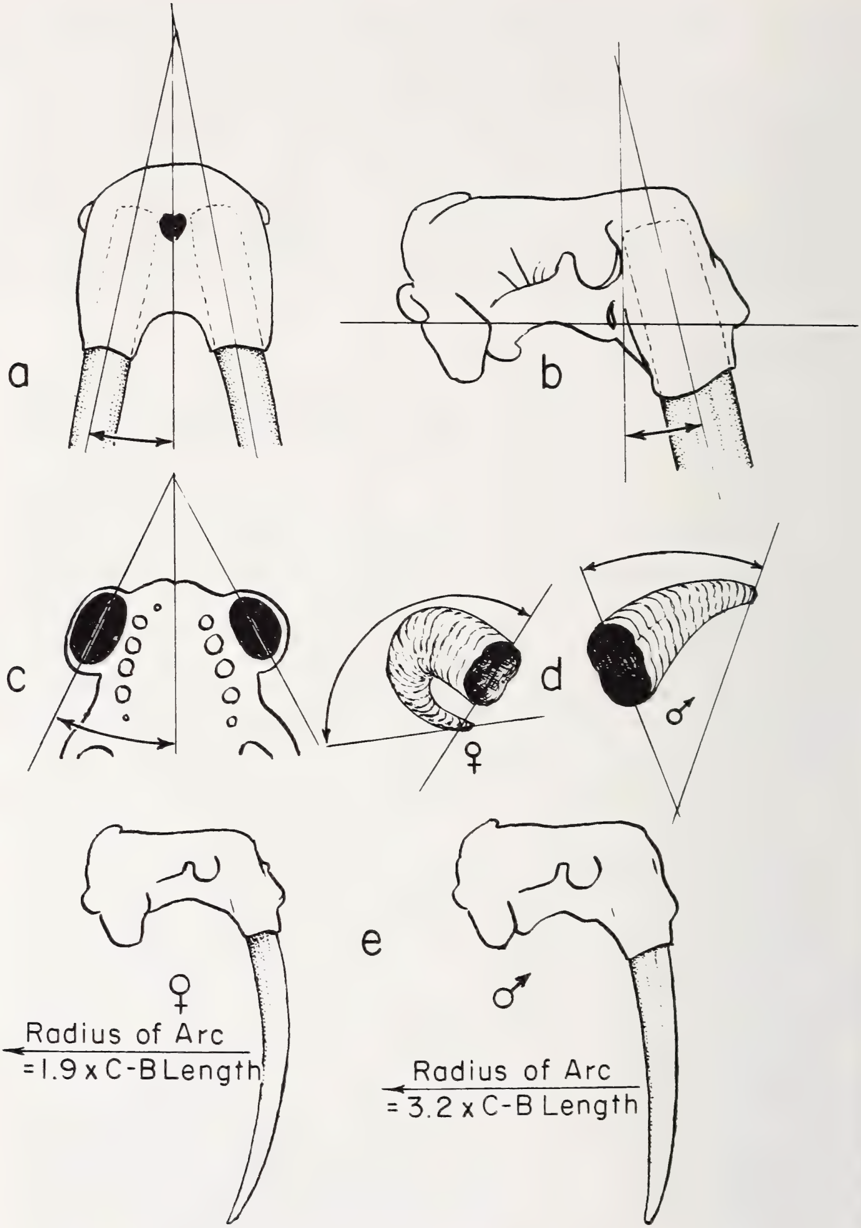

Fig. 75. Examples of orientation and shape of walrus tusks, in relation to sagittal and transverse planes of the skull: (a) inclination in anterior view; (b) inclination in lateral view; (c) angle of the long, cross-sectional axis in ventral view; (d) helical twist in dorsal view; and (e) radius of arc in lateral view.
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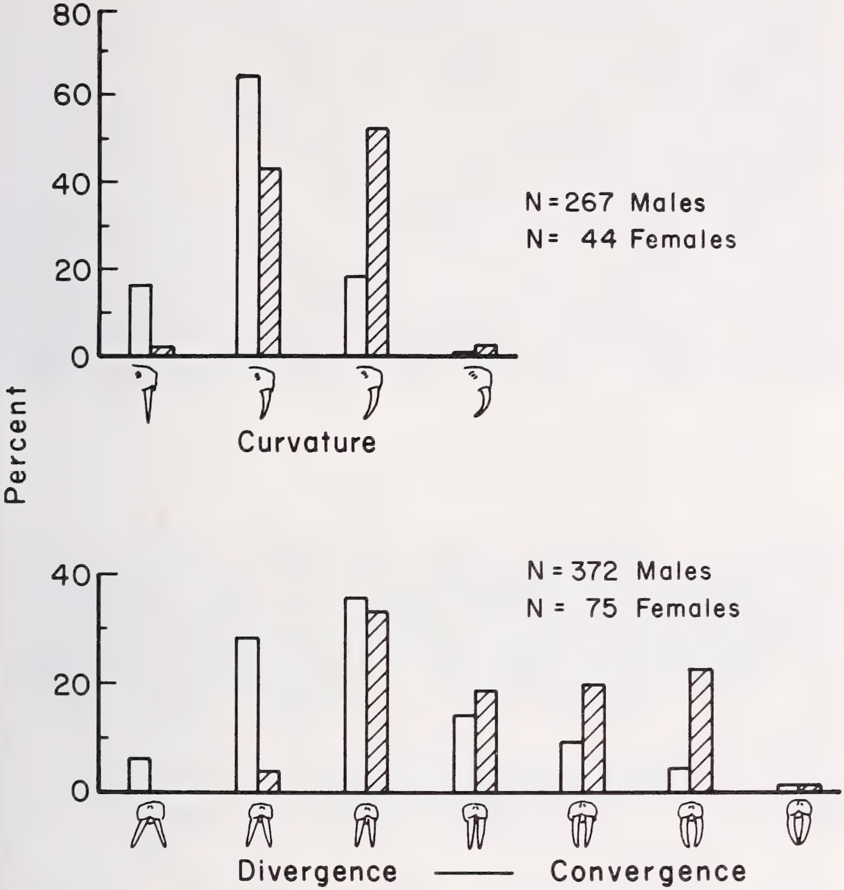


Fig. 76. Comparative curvature and divergence–convergence of tusks of male (open bars) and female (crosshatched bars) Pacific walruses.

nicely symmetrical, with tips that meet or, less often, cross over (Fig. 77). Those of males of comparable age generally are strongly divergent.

As noted earlier, the tusks are elliptical in cross section, with the long axis of the ellipse usually at an angle of 25 to 30° from the sagittal plane. In very young walruses, the length of the long axis of the ellipse at the gingival margin is only about two-thirds of that at the proximal (apical) end of the root (Fig. 78). In older walruses, the conical shape of the tusk is increasingly attenuated as the tusks grow rapidly in length but not proportionately in diameter. The point of equality between the gingival and apical diameters is reached in the tusks of females when the clinical crown is about 25 to 30 cm long (at about 10 years of age); in males it is reached when the crown is about 35 to 40 cm long (about 15 years of age). Thereafter, with increasing age and decreasing linear growth, the tusks tend to become progressively more spindle-shaped, with maximal cross-

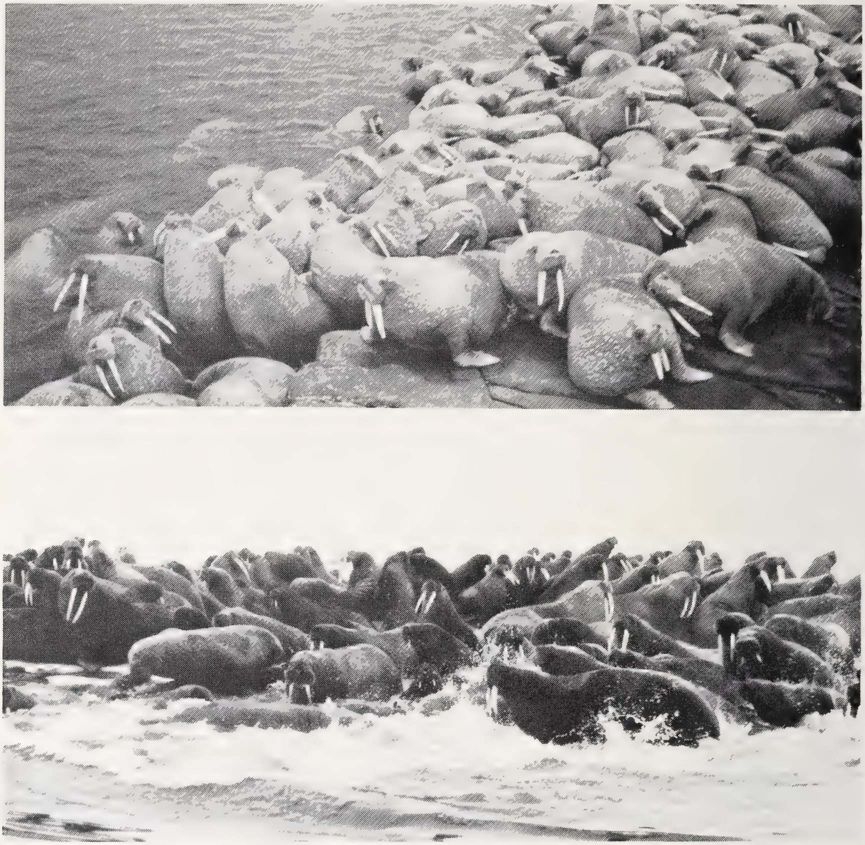


Fig. 77. Comparative views of shape of the tusks in adult male (upper) and female (lower) Pacific walruses. (Photos by K. W. Kenyon and K. J. Frost)

sectional diameter at the gingiva and lesser diameters both proximally and distally. This increase in relative size at the gingiva is mainly a function of increasing extent of overlap of the annual layers of cementum, as noted earlier.

The tusks of males also are stouter and more elliptical than those of comparable length from females (Figs. 79, 80). In both sexes, the cross-sectional area of the tusks at the gingival margin increases with increasing length, but it usually is about 20% greater in males than in females for any given length. In adult males, the ratio of the short to the long axis of the cross-sectional ellipse usually is about 1:1.5, whereas in females it is about 1:1.4. In both sexes, the ratio is least in the immature and greatest in the very old individuals.

Linear Growth, Abrasion, and Fracture of Tusks

The tusks grow and erupt continually, in which respects they are comparable to the incisors of rodents, elephants, and a few other mammals. Their growth is cumulative; new increments are added at the proximal end of the tusk, resulting

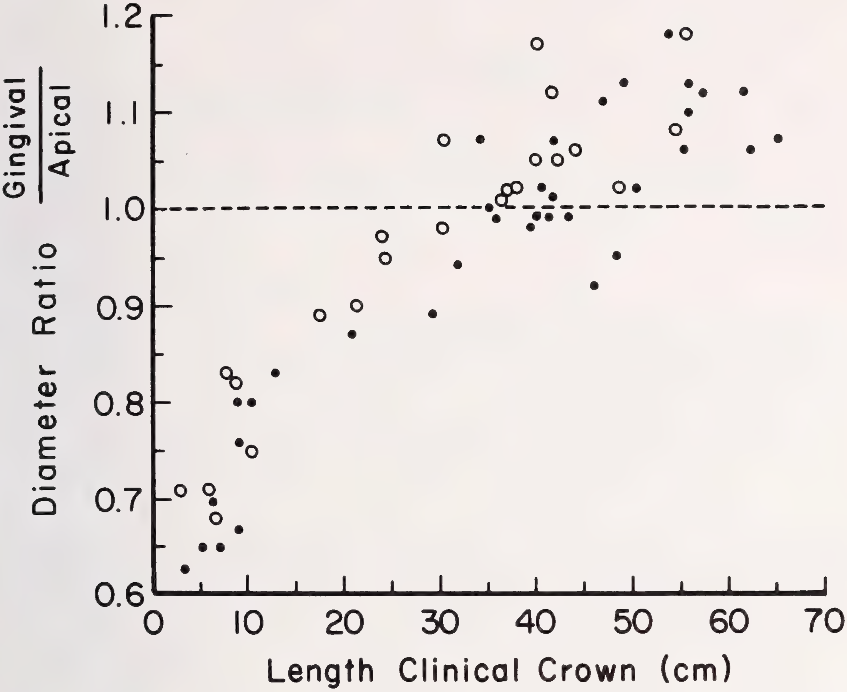


Fig. 78. Ratio of cross-sectional diameter (long axis) of tusks at the gingival margin to that at the root apex, in relation to length of the clinical crown in Pacific walruses. Each point represents one male (dot) or female (circle). Dashed line indicates level of unity of diameters.

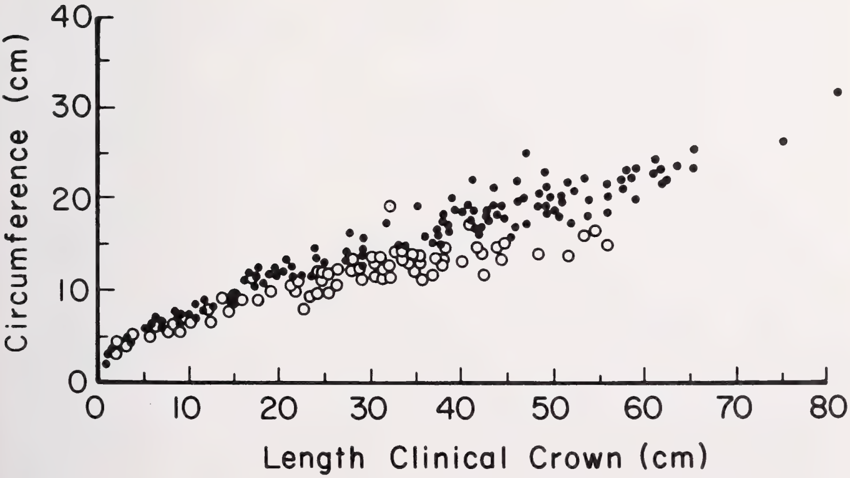


Fig. 79. Comparative stoutness of tusks of male (dots) and female (circles) Pacific walruses, in relation to length of the clinical crown. Each point represents one specimen.

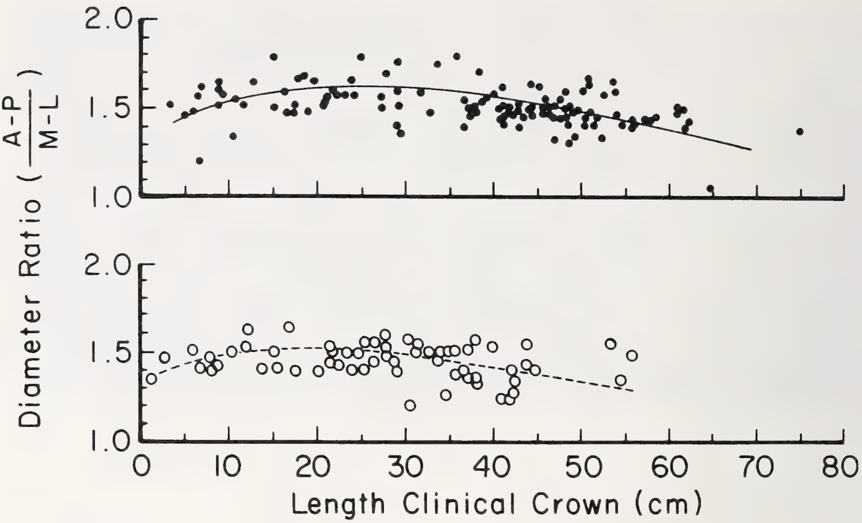


Fig. 80. Change in cross-sectional shape of the tusks, in relation to length of the clinical crown in Pacific walruses. Shape of the cross-sectional ellipse is indicated by the ratio of diameters on the long (A–P) to the short (M–L) axis, measured at the gingival margin. Each point represents one male (dot) and female (circle). Curves were fitted visually.

in a continual increase in length as well as in mass with increasing age. The principal tissue added is dentin, which is deposited on the walls of the pulp chamber in dense layers, and in the central core of the tusk in the form of coalescing globules, as noted earlier. Thin layers of cementum are deposited on the external surface of the clinical root, adding further to the mass but not to the length of the tusk. Ideally, the growth of the tusks should be described in terms of volume or mass. However, for reasons of expediency, I measured only the growth in length.

The length of each tusk is a segment of an arc, rather than a straight line. For that reason, I measured each specimen along the arc of the anterior surface of the tusk, from the gingival margin to the distal tip. This is the *length of the clinical crown* or "exposed length." From many specimens, I was able to remove the tusk from its socket and measure the *length of the clinical root* as well, also along the anterior surface from the gingival margin to the apical end. The sum of those two measurements is the *total length* of the tusk. The total length of the extant tusk, plus the length of material abraded or fractured from its distal end is the *sum of linear increments*. This is the total length that would have been present had there been no decrements. The linear amount of decrement was estimated by direct, visual comparison of abraded or broken tusks with others that were of comparable form but from which little or no tissue had been removed.

Each tusk measurement was correlated with the age of the animal. The results were as follows:

Length of clinical crown.—The tusks first penetrate the gingiva in the summer or autumn after birth; in the next 15 years, the clinical crown increases in length

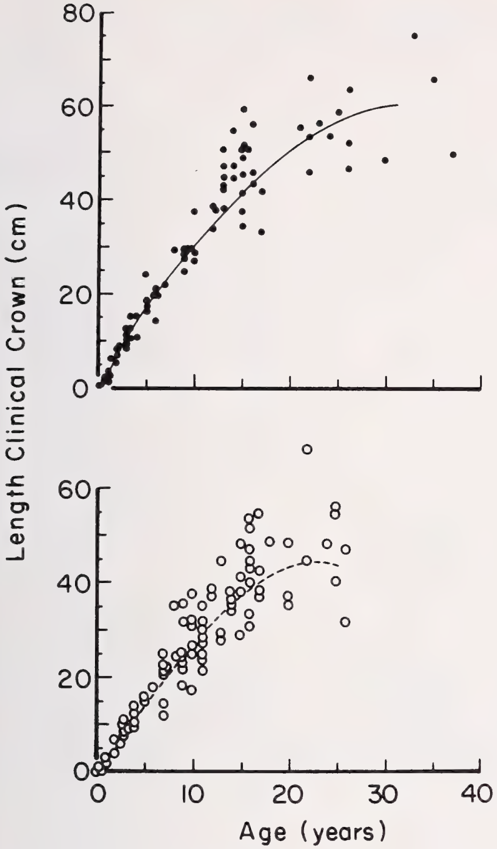


Fig. 81. Length of the clinical crown of the tusks of male (dots) and female (circles) Pacific walruses, in relation to age. Each point represents the longest tusk in one specimen. Curves were fitted visually.

nearly in direct arithmetic relation to age (Fig. 81). This increase takes place both in males and in females; its rate is slightly higher in the males. After about 15 years, the increase slows in males and virtually ceases in females.

The tusks of males tend to be slightly longer than those of females of comparable age. The mean difference usually is no more than about 3 or 4 cm, up to about the 20th year; thereafter it may be as much as 10 cm. With few exceptions, the length of the clinical crown of mature males 15 years old and older ranges from about 35 to 65 cm and that of mature females from 25 to 55 cm. Maximum lengths in my series were 75 cm in a male and 68 cm in a female.

Length of clinical root. —The clinical root of the tusk is the portion proximal to the gingival margin and enclosed within the socket. By this definition, the entire unerupted tusk of fetal and newborn walruses is included, whereas only the proximal part of the tusk is included in older animals. The length of the clinical root is a function of the growth of the skull as well as of the tusk itself; as the skull increases in size, the socket increases in depth. Increase in length of the clinical root takes place for about 10 years in females and 15 years in males, after which it reaches an asymptote of about 19 cm in males and 15 cm in females (Fig. 82).

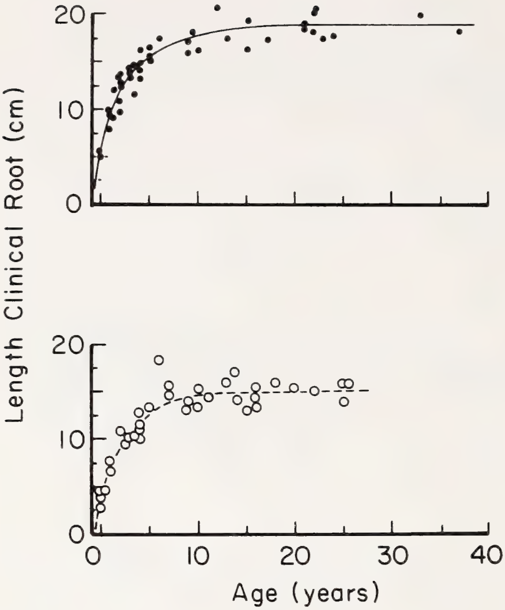


Fig. 82. Length of the clinical root of the tusks of male (dots) and female (circles) Pacific walruses, in relation to age. Each point represents one specimen. Curves were fitted visually.

Total length.—The total length of the tusks is the overall measurement from root apex to distal tip, or the sum of the clinical crown and clinical root. Sexual dimorphism is more apparent here than in the length of the clinical crown alone (Fig. 83). Maximum total length for tusks of males exceeds 1 m; the maximum in females probably is about 80 cm.

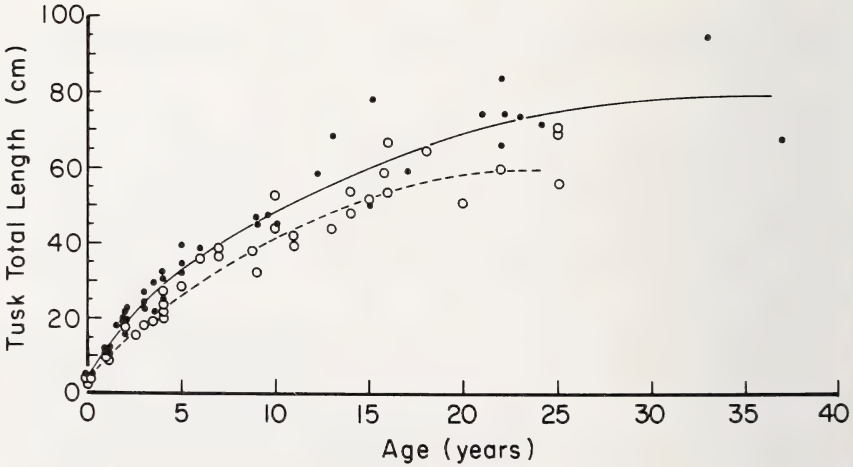


Fig. 83. Total length of tusks of male (dots) and female (circles) Pacific walruses, in relation to age. Each point represents one specimen. Curves are based on sums of those in Figs. 81 and 82.

Table 13. *Measurements and estimated sum of linear increments for tusks of 28 immature male Pacific walruses.*

	Length (mm)			
Age (years)	Clinical crown	Clinical root	Lost by abrasion	Estimated sum of increments
0.0	0	51	0	51
0.0	0	52	0	52
0.0	0	54	0	54
0.3[a]	0	65	0	65
0.4[a]	10	72	0	82
1.0	19	96	0	115
1.0	22	95	0	117
1.1	29	79	2	110
1.2[a]	14	98	0	112
1.2	33	90	2	125
1.3[a]	31	105	1	137
1.5	63	121	5	189
2.0	51	110	9	170
2.0	70	124	6	200
2.0	64	133	6	203
2.0	89	135	7	231
2.0	90	97	6	193
3.0	106	142	5	253
3.0	89	135	7	231
3.0	127	140	10	277
3.5	152	146	19	317
3.6	105	115	18	238
4.0	108	149	13	270
4.0	152	162	25	339
4.0	159	143	20	322
5.0	184	165	50	399
6.0	209	175	25	409
9.0	292	172	50	514

[a] Walruses of known age reared in captivity.

Rate of linear growth.—The length of the annual increments of tusk growth can be measured as the distance between the successive annular ridges on the root, the latest increment being most proximal. In immature walruses, distinct annulations usually are not recognizable with certainty, but because the tusks are only lightly abraded, they make up nearly the entire sum of linear increments. The few millimeters of length that have been lost through abrasion can be estimated by visual comparison with tusks of similar form from younger animals. Using those measurements (Tables 13, 14), I derived estimated annual linear increments of tusk growth for the pre-adult years. Annual increment rates for the adult years were measured directly as the distances between annular ridges.

I obtained the longest series of measured increments from tusks that I decalcified, then stripped away the cementum (Fig. 84). Shorter series were measured on longitudinally sectioned tusks; the shortest series were measured on

Table 14. *Measurements and estimated sum of linear increments for tusks of 24 female Pacific walruses.*

Age (years)	Length (mm) Clinical crown	Clinical root	Lost by abrasion	Estimated sum of increments
0.0	0	30	0	30
0.0	0	42	0	42
0.0	0	42	0	42
0.0	0	44	0	44
0.0	0	45	0	45
0.0	0	45	0	45
0.0	0	45	0	45
1.0	13	79	0	92
1.0	29	67	0	96
1.2[a]	25	75	11	111
1.3[a]	22	75	3	100
2.0	67	108	6	181
2.6	60	97	6	163
3.0	79	102	10	191
3.4[a]	28	101	100	229
3.5	89	104	11	204
4.0	99	103	18	220
4.0	105	114	16	235
4.0	140	127	19	286
4.0	124	111	10	245
5.0	152	133	19	304
6.0	177	183	25	385
7.0	216	146	29	391
8.8	245	131	100	476

[a] Walruses of known age reared in captivity.

tusks that had not been treated by either of those methods. Average annual increments from the tusks of 11 males and 11 females (from which two or more measurements were made) ranged from 33.4 mm at age 13 to 3.5 mm at age 33 for males (Table 15) and from 43.0 mm at age 8 to 2.5 mm at age 25 (Table 16). Possibly, the increments from the females are atypical, for they were from the only tusks in a large series that had well expressed annular ridges on the roots.

The incremental rates derived graphically from Tables 13 and 14 and from the mean increments in Tables 15 and 16 were plotted, and smoothed curves were fitted to them (Fig. 85). The results for both sexes suggest that growth in length of the tusks accelerates for about 2 years after birth and then decelerates in three or four stages during the remainder of life. The final stage of rapid deceleration seems to begin about the 28th or 29th year in males and about 10 years earlier in females. In both sexes, the maximum increment (second year) is about 6 to 8 cm; the most usual rate in adulthood is between 1 and 3 cm per year. In very old animals, the increment may be as little as 1 mm per year.

Rate of decrement.—To obtain an estimate of relative rates of decrement of tissue from the tips of the tusks at different ages, I compared total length with the

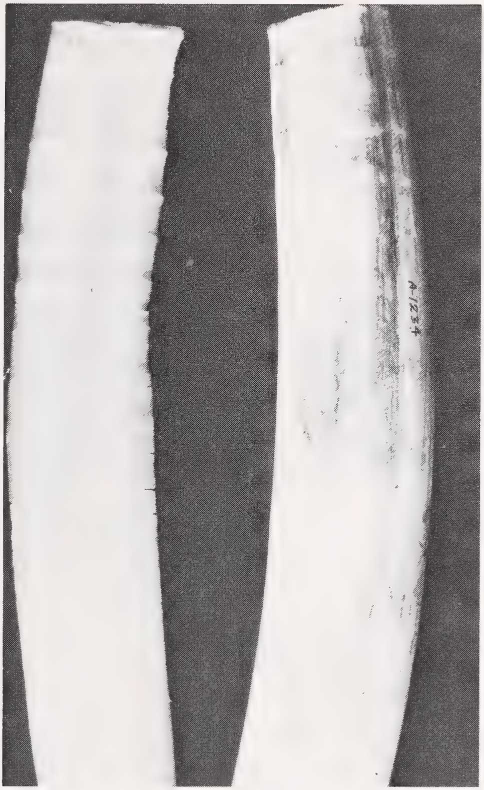


Fig. 84. Exposure of linear dentinal increments in a tusk from an adult male Pacific walrus. Right, basal part of untreated tusk on which five annular ridges are visible near the apical end (upper); left, decalcified slab sawn from the opposite side of the same tusk, showing five additional ridges that were exposed by removal of the cementum. (Photo by F. H. Fay)

sum of linear increments. The results (Tables 17 and 18) suggest that the rate of decrement is higher from tusks of males than from those of females, and the highest rates in both sexes are in the weanling to subadult years, when the tusks are most slender and divergent and the tips jut forward to or beyond the anterior plane of the snout.

Because the tusks of females are more slender than those of males, one might expect them to be shortened more rapidly by abrasion, but this does not seem to happen. The high rate of decrement from the tusks of the immature animals suggests that the tips have the greatest exposure to abrasive materials at that age.

Fracture.—Minor breakage or flaking of the tips of the tusks occurs rarely in immature walruses, infrequently in adult females, and very frequently in adult males. This may account in part for the apparently higher overall rate of linear decrement from the tusks of males. The causes of this flaking are not completely known. Where males haul out on rocky shores in summer, impact against the rocks may be a major cause. Many of the bulls residing at Round Island in summer showed signs of recent fracture, and J. W. Brooks, K. W. Kenyon, and I retrieved several fragments of tusks from among the rocks there. The smallest fragments were flakes a few millimeters long; the largest was nearly the entire clinical crown broken off near the base. J. Harkey, W. Sholes, and E. H. Miller

Table 15. *Series of annual linear increments (mm) measured on tusks of 11 male Pacific walruses.*

Year of age	Condition of tusk, and animal no.												
	Untreated tusks						Decalcified tusks					Sample	
	1	2	3	4	5	6	7	8	9	10	11	Size	Mean
8	—	—	—	—	—	—	40	—	—	—	—	1	40.0
9	—	—	—	—	—	—	26	33	—	—	—	2	29.5
10	—	—	—	—	—	—	33	29	—	—	—	2	31.0
11	—	—	—	—	—	—	30	30	—	—	—	2	30.0
12	31	—	—	—	—	—	28	25	39	41	—	5	32.8
13	—	30	25	—	—	—	24	27	40	42	46	7	33.4
14	—	30	25	—	—	—	25	20	38	30	28	7	28.0
15	—	26.5	22	—	—	—	25	17	32	27	28	7	25.4
16	—	22.5	19	—	—	—	24	13	—	20	25	6	20.6
17	—	24	19	—	—	—	22	14.5	—	21	25	6	20.9
18	—	26	16	—	—	—	24	15	—	21	24	6	21.0
19	—	20.5	19	19	25	—	25	16	—	20	22	8	20.8
20	—	24	19	15	25	33	24	15	—	19	20	9	21.6
21	—	22	19	17	25	29	26	12.5	—	19	23	9	21.4
22	—	—	16	13.5	22	—	20	11.5	—	16	—	6	16.5
23	—	—	16	—	—	—	18	11.5	—	16	—	4	15.4
24	—	—	—	—	—	—	19	10	—	16	—	3	15.0
25	—	—	—	—	—	—	17	10.5	—	—	—	2	13.8
26	—	—	—	—	—	—	12	9.5	—	—	—	2	10.8
27	—	—	—	—	—	—	13	11.5	—	—	—	2	12.2
28	—	—	—	—	—	—	13	9	—	—	—	2	11.0
29	—	—	—	—	—	—	10	6.5	—	—	—	2	8.2
30	—	—	—	—	—	—	8	6	—	—	—	2	7.0
31	—	—	—	—	—	—	8	3.5	—	—	—	2	5.8
32	—	—	—	—	—	—	6	3	—	—	—	2	4.5
33	—	—	—	—	—	—	4	3	—	—	—	2	3.5
34	—	—	—	—	—	—	—	2.5	—	—	—	1	2.5
35	—	—	—	—	—	—	—	1.5	—	—	—	1	1.5
36	—	—	—	—	—	—	—	1	—	—	—	1	1

Table 16. *Series of annual linear increments (mm) measured on tusks of 11 female Pacific walruses.*[a]

Year	Animal no.											Sample	
of age	1	2	3	4	5	6	7	8	9	10	11	Size	Mean
5	50	—	—	—	—	—	—	—	—	—	—	1	50.0
6	47	37	—	—	—	—	—	—	—	—	—	2	42.0
7	34	40	—	—	—	—	—	—	—	—	—	2	37.0
8	—	38	48	—	—	—	—	—	—	—	—	2	43.0
9	—	30	38	21	22.5	—	—	—	—	—	—	4	27.9
10	—	32	13	17	20	—	—	—	—	—	—	4	20.5
11	—	34	29	—	17	—	—	—	—	—	—	3	26.7
12	—	—	22	—	18	17	—	—	—	—	—	3	19.0
13	—	—	38	—	17	19	19	—	—	—	—	4	23.2
14	—	—	—	—	17.5	17	13	—	—	—	—	3	15.8
15	—	—	—	—	—	18	13	13	—	—	—	3	14.7
16	—	—	—	—	—	—	19	13	—	—	—	2	16.0
17	—	—	—	—	—	—	13	—	21	—	—	2	17.0
18	—	—	—	—	—	—	13	—	20	—	—	2	16.5
19	—	—	—	—	—	—	10	—	—	—	—	1	10.0
20	—	—	—	—	—	—	9	—	—	—	—	1	9.0
21	—	—	—	—	—	—	6	—	—	4.5	—	2	5.2
22	—	—	—	—	—	—	6	—	—	3.5	—	2	4.8
23	—	—	—	—	—	—	6	—	—	3.5	—	2	4.8
24	—	—	—	—	—	—	—	—	—	3	—	1	3.0
25	—	—	—	—	—	—	—	—	—	2	3	2	2.5

[a] Untreated tusks only.

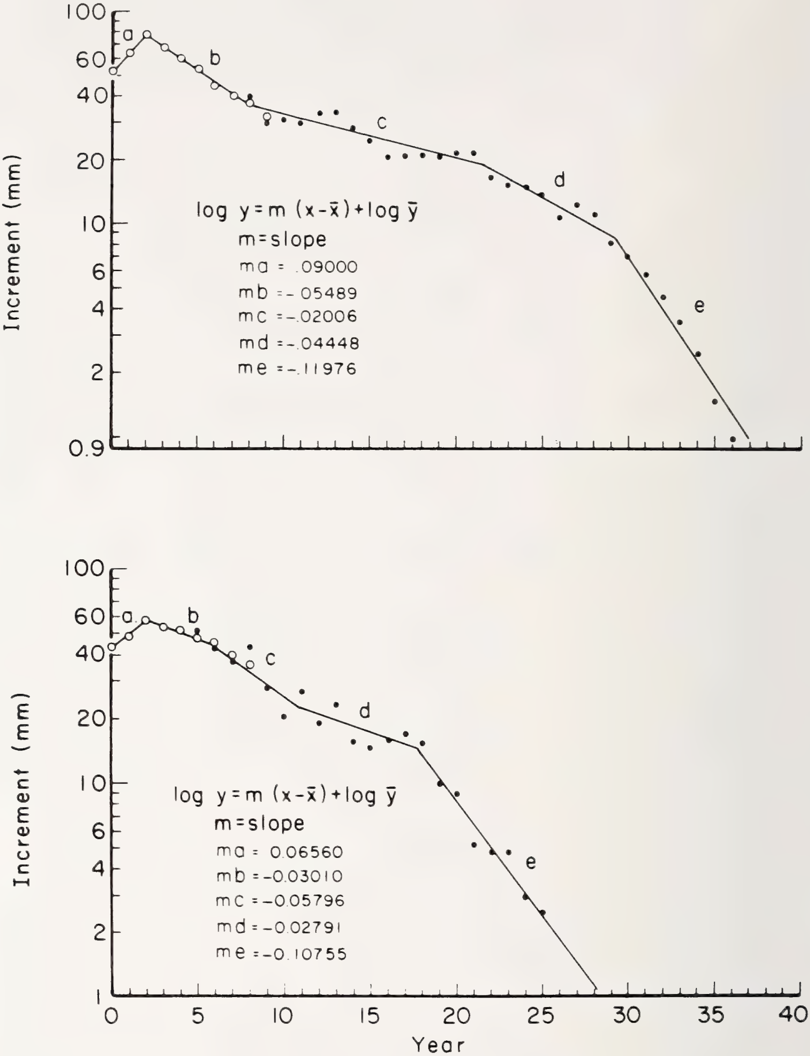


Fig. 85. Estimated mean annual increments of linear growth in tusks of male (upper) and female (lower) Pacific walruses. Values derived graphically from data in Tables 13 and 14 (circles) and from means in Tables 15 and 16 (dots). Curves were fitted by the method of least squares. Slope constants (m) for each segment are shown at left.

(personal communication) reported similar findings in rocky areas at St. Lawrence and Round islands. Fracture of tusks takes place also at sea, for I have seen several bulls with newly broken tusks, far out in the ice during the winter. I suspect that these were fractured in the course of agonistic encounters, for the tusks of opponents often strike resoundingly during threat and subsequent

Table 17. *Estimated rates of decrement from tusks of male Pacific walruses.*

	Tusk length (cm)		Decrements (cm)	
Age (years)	Total[a]	Sum linear increments[b]	Total	Annual rate
0	5.1	5.1	0.0	0.0
1	11.4	11.4	0.0	0.0
2	18.5	19.1	0.6	0.6
3	24.5	25.9	1.4	0.8
4	29.0	31.8	2.8	1.4
5	32.8	37.1	4.3	1.5
6	36.2	41.7	5.5	1.2
7	39.3	45.8	6.5	1.0
8	42.1	49.4	7.3	0.8
9	45.0	52.8	7.8	0.5
10	47.8	56.1	8.3	0.5
11	50.4	59.2	8.8	0.5
12	52.9	62.1	9.2	0.4
13	55.5	65.0	9.5	0.4
14	57.8	67.7	9.9	0.4
15	60.0	70.3	10.3	0.4
16	62.1	72.8	10.7	0.4
17	64.0	75.1	11.1	0.4
18	65.9	77.4	11.5	0.4
19	67.6	79.5	11.9	0.4
20	69.3	81.6	12.3	0.4
21	70.8	83.5	12.7	0.4
22	72.3	85.4	13.1	0.4
23	73.5	87.0	13.5	0.4
24	74.6	88.5	13.9	0.4
25	75.5	89.8	14.3	0.4
26	76.4	91.0	14.6	0.3
27	77.2	92.1	14.9	0.3
28	77.9	93.1	15.2	0.3
29	78.5	94.0	15.5	0.3
30	78.9	94.7	15.8	0.3
31	79.1	95.2	16.1	0.3
32	79.2	95.6	16.4	0.3
33	79.2	95.9	16.7	0.3
34	79.1	96.1	17.0	0.3
35	79.0	96.3	17.3	0.3

[a] Total lengths are estimated means from Fig. 83.
[b] Sum of linear increments from fitted curves in Fig. 85.

fighting by males (Miller 1975*a*). Probably that impact is great enough in some instances to cause fracture.

Of 94 bulls with fractured tusks that I saw on Round Island, 67 (71%) had lost all or part of one tusk. Most of those losses involved less than half of the clinical crown. Fracture of both tusks had taken place in 27 (29%), also mostly involving less than half of the crown and most often affecting both tusks about equally.

Table 18. *Estimated rates of decrement from tusks of female Pacific walruses.*

Age (years)	Tusk length (cm) Total[a]	Tusk length (cm) Sum linear increments[b]	Decrements (cm) Total	Decrements (cm) Annual rate
0	4.3	4.3	0.0	0.0
1	9.2	9.2	0.0	0.0
2	14.3	15.0	0.7	0.7
3	18.8	20.4	1.6	0.9
4	22.4	25.5	3.1	1.2
5	26.0	30.2	4.2	1.1
6	29.5	34.5	5.0	0.8
7	32.6	38.3	5.7	0.7
8	35.7	41.6	5.9	0.2
9	38.5	44.5	6.0	0.1
10	41.1	47.0	5.9	0.0
11	43.6	49.3	5.7	0.0
12	45.6	51.4	5.8	0.0
13	47.8	53.4	5.6	0.0
14	50.0	55.2	5.2	0.0
15	51.8	57.0	5.2	0.0
16	53.6	58.6	5.0	0.0
17	55.0	60.2	5.2	0.0
18	56.4	61.5	5.1	0.0
19	57.3	62.6	5.3	0.0
20	58.0	63.5	5.5	0.0
21	58.7	64.1	5.4	0.0
22	59.0	64.9	5.9	0.0
23	59.1	65.0	5.9	0.0
24	58.9	65.3	6.4	0.4
25	58.7	65.6	6.9	0.5

[a] Total lengths are estimated means from Fig. 83.
[b] Sum of linear increments from fitted curves in Fig. 85.

Fractures tended to occur most often in males who had curved, highly divergent tusks (Fig. 86). Fractured tusks also tended to occur more often in mature males (94/267) than in subadult males (10/103). This difference probably reflects increasing likelihood of fracture with increasing age. Major fracture of the tusks of females seems to occur less often than in males, possibly because females avoid haulouts on rocky shores or engage in less vigorous fights. In a sample of 79 adult females sighted at sea, only 2 showed fractures; in both, these were of one tusk.

I saw bilateral fractures of the tusks about 35 to 40 cm distal to the gingiva in several old females (Fig. 87, right). The site of these fractures was at or just distal to the most anterior point in the parasagittal arc. In old females, the loss of tissue by frontal abrasion in that area results in great reduction in thickness of the shaft. Sometimes the shaft is thinner there than near the tip (Fig. 87, left). Moderate pressure or light impact are sufficient to break the tusk at this weak point, as I discovered accidentally while examining one dead specimen in the field. The development of the weak point seems to be due to two factors: frontal

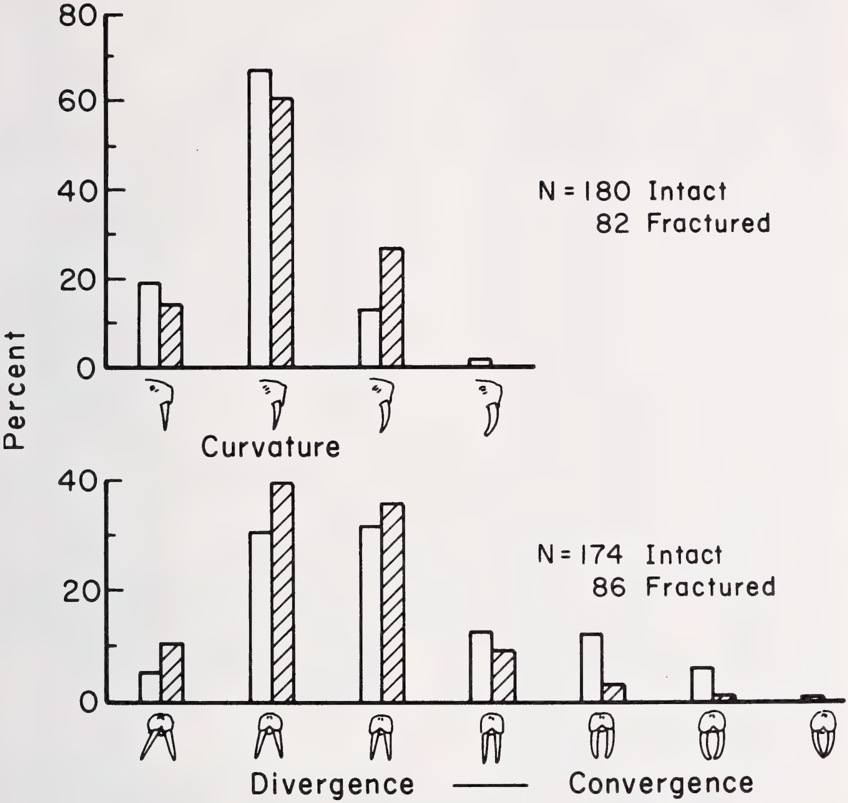


Fig. 86. Comparative shapes of intact (open bars) and fractured (crosshatched) tusks of adult male Pacific walruses.

abrasion and the slow rate of linear growth of the tusks in old age. Frontal abrasion of the tusks is normal throughout the lifetime of these animals. Its greatest effect is on or below the anteriormost part of the parasagittal arc. While the tusks are rapidly growing in young animals, the area affected by that abrasion is continually changing. However, when growth is very slow in the old animals, the abrasion is on nearly the same area for several years in succession, resulting in extreme reduction in thickness at that point.

Abraded Surfaces of Tusks

The form of the clinical crown of the tusks is continually altered by abrasion, presumably during contact with the mud, sand, and gravel of the sea floor while the animals are feeding. The principal effects of this are increased proximal-to-distal taper and reduced length of the crown. The greatest effects of abrasion are apparent on the anterolateral surface, near the distal end (Fig. 88*a*). There, the outer layers of cementum and dentin are worn away, exposing the core to view.

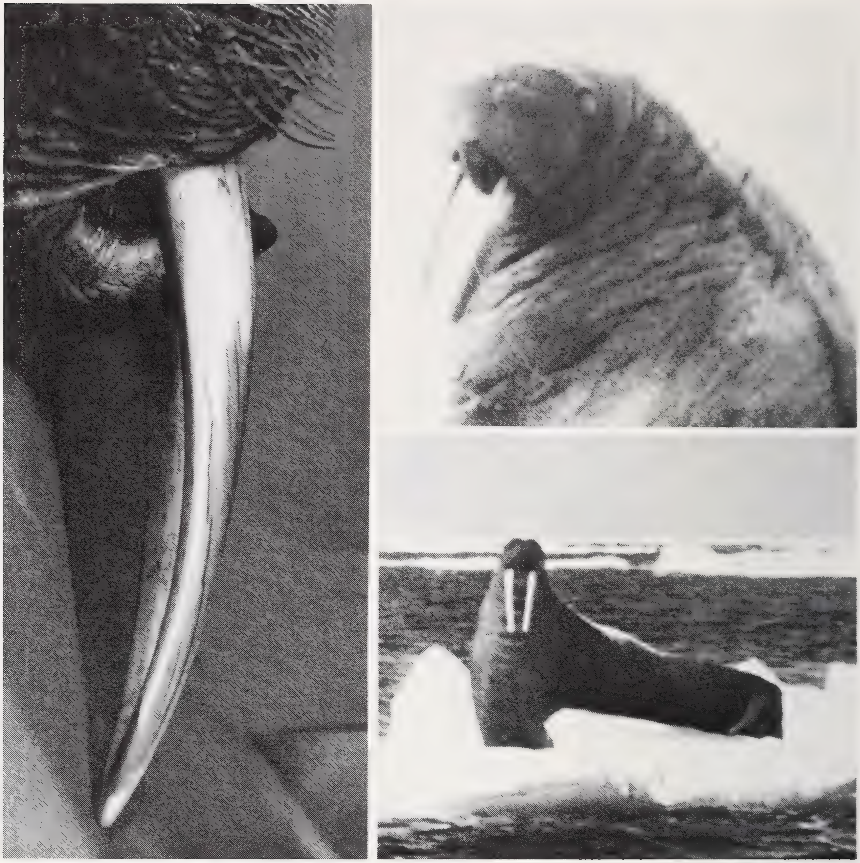


Fig. 87. Frontal abrasion and fracture of tusks of female Pacific walruses in old age: left, tusks of a 25-year-old female in which the distal third of the crown has been weakened by frontal abrasion; right, old females from which the distal part of the weakened tusks has been lost due to bilateral fracture. (Photos by F. H. Fay)

The posteromedial surface is least affected and often remains nearly intact all the way to the tip. (Fig. 88*b*). The posterior surface sustains about twice as much tissue loss as the medial surface, and the lateral surface about six times as much. The principal vector of abrasive force affecting the tusks is at an angle of about 25° from the sagittal plane of the head, rather than parallel to that plane (Fig. 89*b*). This vector is exactly perpendicular to the frontal plane of each side of the snout, immediately above the tusks (Fig. 89*a*).

The anterolateral surface of each tusk is densely pitted by the most direct impact of abrasive particles (Fig. 90, left). The principal direction of movement of those particles along that surface is distad, as indicated by the striations made by the particles. On the lateral and medial surfaces, the striae indicate posterodistad movement of the abrasives. The striae there mostly are oriented at 10 to 50° from the long axis of the shaft; the predominant angle is about 35°

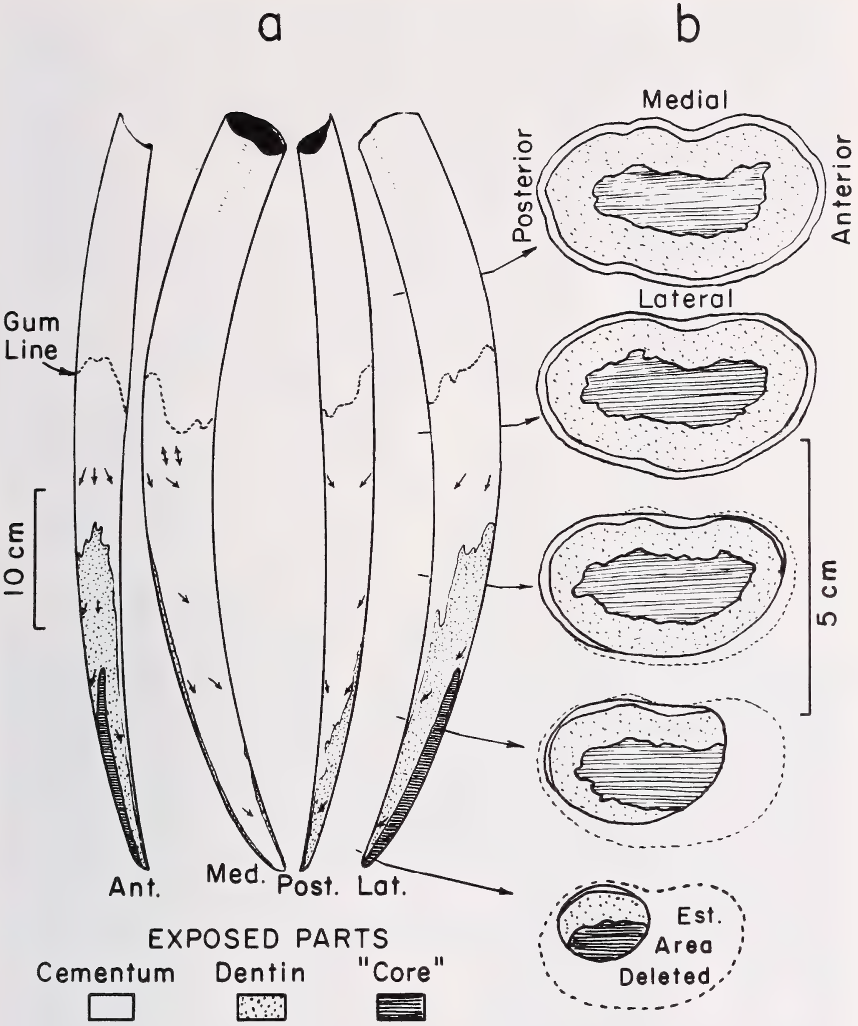


Fig. 88. Diagrammatic views of the patterns of abrasion and decrement of the clinical crown of a tusk from a 15-year-old female Pacific walrus: (a) anterior, medial, posterior, and lateral aspects of the right tusk, showing paths of abrasive particles (arrows) and resultant exposure of the deep tissues; and (b) cross-sections of the same tusk at 10-cm intervals.

(Figs. 88*a*; 90, center). On the posterior surface, the striae tend to converge obliquely distad.

The pattern of striae described above is evident on most tusks along the full length of the clinical crown. It tends to be most clearly expressed on the tusks of females and immature males; in adult males, it sometimes is obscured by massive engraving by coarser particles with no predominant orientation of striae. Pitting

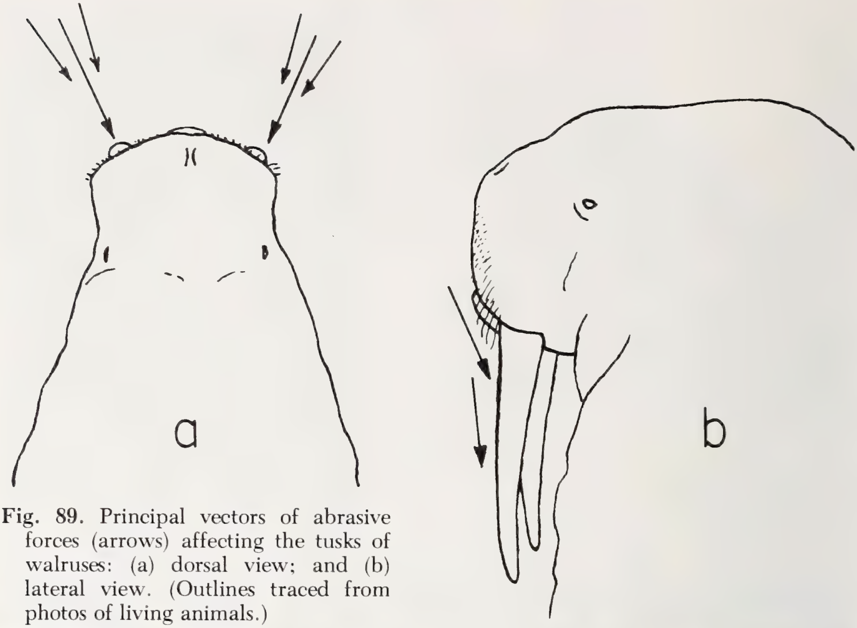


Fig. 89. Principal vectors of abrasive forces (arrows) affecting the tusks of walruses: (a) dorsal view; and (b) lateral view. (Outlines traced from photos of living animals.)

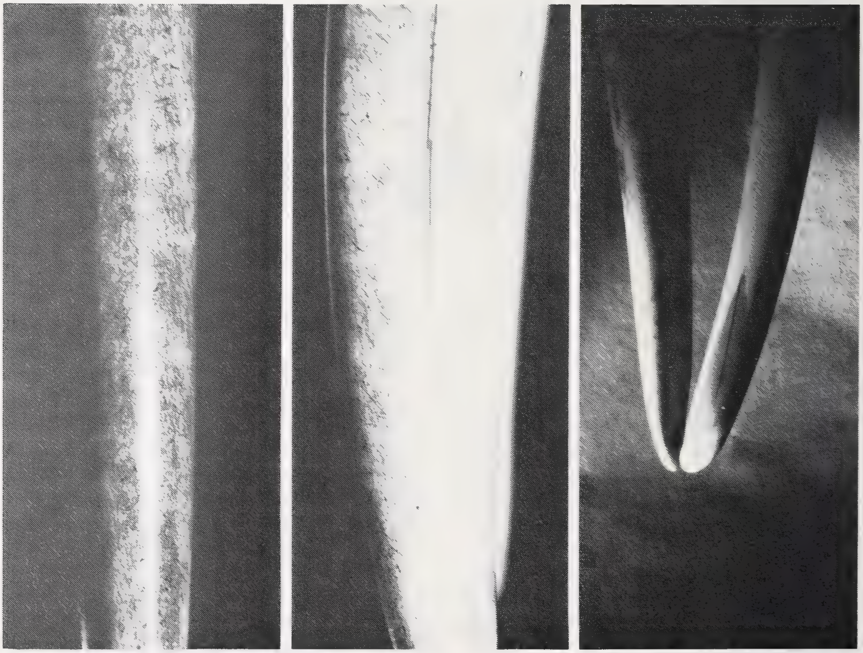


Fig. 90. Examples of abraded surfaces of tusks of Pacific walruses: left, anterior aspect, showing pitted surface; center, lateral aspect, with diagonal striae on the tusks of a 10-year-old female; and right, polished tip on the posterodistal aspect of the tusks of a 25-year-old female. (Photos by F. H. Fay)

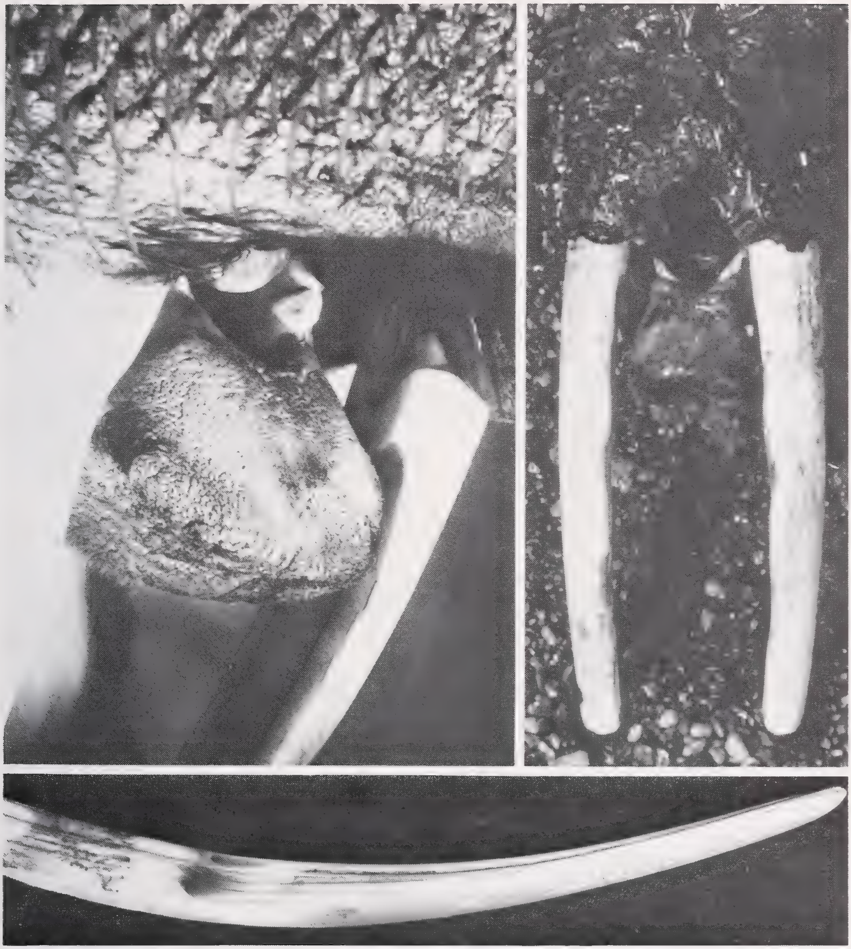


Fig. 91. Focal abrasion on the medial surface of the tusks: left, anteromedial view of the mouth of a 25-year-old female, showing foci of medial abrasion adjacent to the lower jaw; right, anterior view of the tusks of an old female in which are two deeply worn foci of medial abrasion in the distal half and one broader focus proximally; lower, anteromedial view of the right tusk of an old female, showing deep medial abrasion. (Photos by F. H. Fay and G. C. Kelley)

of the anterior surface usually is most intense in adult males.

In most males and in nearly all females, the posterior aspect of the tip of each tusk is smooth and often highly polished (Fig. 90, right). This burnishing apparently is caused by frequent contact with the skin of the breast, for the polish is most intense on those tusks with the greatest parasagittal curvature.

Loss of tissue by abrasion takes place also on the medial surface of the tusk, where it contacts the lower jaw (Fig. 91). The material removed is mainly cementum, and the primary site of this abrasion is just distal to the gingiva, where it appears as a shallow depression. The depression usually is highly polished and has a few, fine striae parallel to the long axis of the shaft. Abrasion apparently takes place there as a consequence of movement of the mandible, presumably while feeding, and probably is hastened by the presence of benthic sediments caught between the lower jaw and the tusk.

Medial abrasion of this type probably takes place continuously throughout the lifetime of the animal. During the preadult years, when linear growth of the tusks is most rapid, this abrasion smooths and polishes the medial surface of the shaft and creates slight undulations in it. On the tusks of many adult males, however, a series of shallow depressions is produced, the regularity and dimensions of which suggest direct relation with the annual cycle of linear growth of the tusks.

Much deeper, more irregularly spaced depressions of this kind often are present along the medial surface of the tusks of middle-aged and older females. The spacing of these, mostly 3 to 7 cm apart, does not correlate with the annual cycle of linear growth but suggests that they are formed at 2- to 5-year intervals. Since such intervals correspond to those between pregnancies, I suspect that these deep depressions are produced during periods of intensive feeding, probably during the late prenatal period. In a pregnant walrus held in captivity ("Petula": Marineland of the Pacific), maximal food intake took place from February to the time of birth in June (E. D. Asper, personal communication).

I found the deepest depressions of medial abrasion on the tusks of very old individuals. These penetrated through the cementum and well into the dentin. Apparently, they resulted from continuous abrasion over a period of several years on virtually the same locus, for the tusks of these animals all showed linear growth rates of less than 3 mm per year. That this extreme abrasion can lead to weakening of the tusks was indicated by fractures at that locus in each of two very old bulls that I observed on Round Island.

Missing and Anomalous Tusks

Of 1,106 specimens, most of them adult males, only 17 (1.5%) lacked one tusk, and 2 (0.2%) lacked both tusks (Fig. 92). Nine of the missing tusks appeared to have been shed, probably due to pulpitis; six of the remainder had been broken off at or just distal to the gingiva. In each of the two animals with no tusks, one tusk apparently had been shed and the other broken off.

I recorded seven instances of anomalous tusks in free-living walruses and was able to determine that four of these were due to abscess of the pulp (Fig. 93); at least three of the remainder were supernumeraries not caused by abscess (Fig. 94). Two of the four pulpal abscesses were caused by bullet wounds; the causes of the other two were not determined. Other instances of tusk anomalies have been reported by Colyer (1936) and Caldwell (1964).

The nature of the abrasion on anomalous tusks suggested that the tusks are dragged through the benthic sediments, rather than used for digging. For example, in one young male that had one normal tusk and one which jutted anteriad, the anomalous tusk had been abraded to about half the length of the other, though they were about equal in basal circumference. The tip of the anomalous tusk was strongly beveled, like the tips of the superior mystacial vibrissae. In each of the specimens that had supernumerary tusks, the anterior-

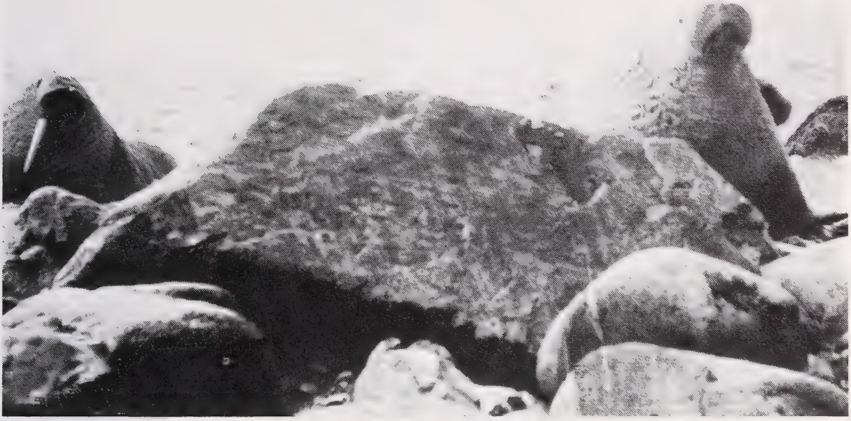


Fig. 92. Absence of tusks in some adult male Pacific walruses. The left tusk of the larger animal (right) had fractured at the gingival level; the right tusk had been shed. The cause of loss of the left tusk from the smaller animal was not determined. (Photo by F. H. Fay)

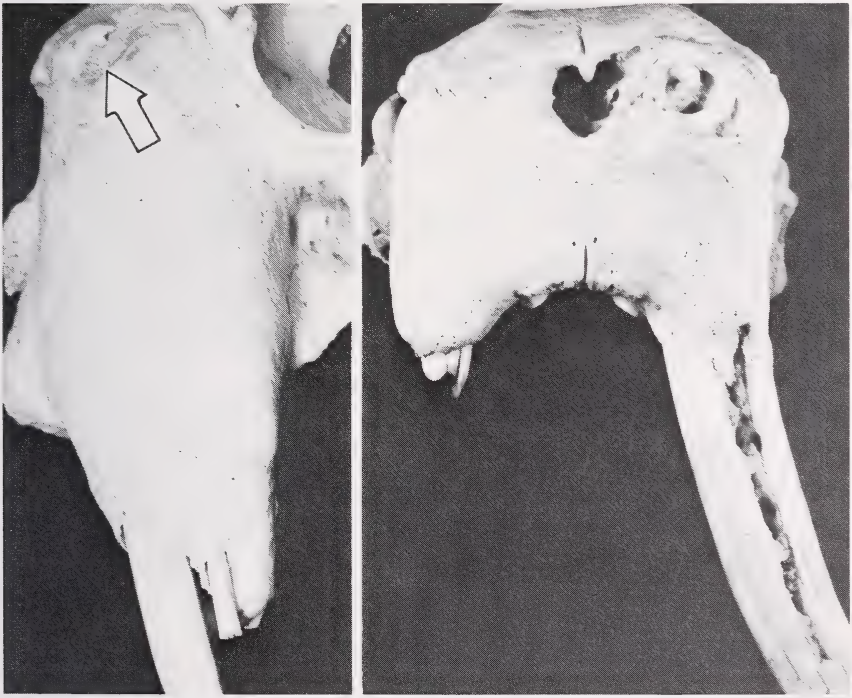


Fig. 93. Tusk anomalies that resulted from infection of the pulp, associated with bullet wounds: left, lateral view of the left maxillary area of an adult female, in which three of the five separate tusks can be seen; pit (arrow) at dorsal end of the socket was the site of the wound; and right, anterior aspect of the skull of an adult male, in which both tusks had draining pulpal abscesses; original wound was at dorsal end of left socket. (Photos by K. L. Austerman)

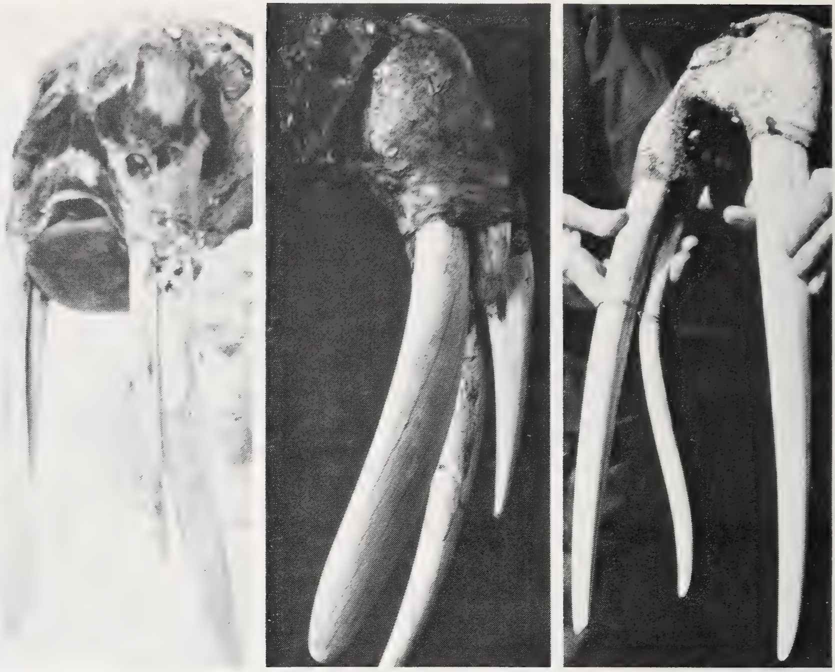


Fig. 94. Examples of naturally occurring supernumerary tusks: left, anterolateral view of the head (skin removed) of an adult female Pacific walrus with bilaterally symmetrical supernumeraries; center, lateral view of the snout (skin and flesh removed) of an adult male Pacific walrus with asymmetrical supernumeraries; and right, oblique view of the tusks of an adult (male?) Atlantic walrus with a large supernumerary behind the apparently normal right tusk. (Photos by F. H. Fay, G. C. Ray, and J. J. Burns)

most tusks were most intensively abraded; the posterior tusks had been shielded from abrasion (Fig. 94).

The frequency of occurrence of anomalous tusks (including supernumeraries) in Pacific walruses certainly is less than 0.1%. From 1952 to 1960, the St. Lawrence Islanders took at least 4,000 walruses, only 2 of which had anomalous tusks; 1 of those had been taken selectively as a curio. At Round Island in July 1974, I observed more than 3,000 males, only 1 of which had an anomalous tusk.

Function of Tusks

Relation to Feeding

For a long time, the principal function of the tusks of the walrus was thought to be in digging or raking up clams. Allen (1880:135) cited "Anderson" as the first to recognize that walruses eat mollusks and that they obtain them "from the bottom of the sea by digging with their tusks." Apparently Cranz (*in* Allen 1880:137) was among the first to accept that hypothesis. Its frequent repetition in scholarly and other works in the meantime has led to its being widely adopted (e.g., Bel'kovich and Yablokov 1961:52; King 1964:40; Walker et al. 1964:1297). Some doubt was cast by Brooks (1954:59) on the importance of the tusks in feeding, for he observed that "an old bull walrus . . . that had no tusks whatever" was in "healthy condition," from which he cautiously concluded that "the tusks may not be absolutely necessary for food procurement." I have seen several adult walruses that lacked tusks, and numerous others in which the tusks were very short. The physical condition of each animal was comparable to that of its tusk-bearing companions, seemingly confirming that tusks are not essential for obtaining food.

Mansfield (1958*a*:69) judged that the predominant anterolateral abrasion of the tusks suggested that the animal uses them for stirring up the benthic sediments while "standing on its head and rotating its tusks from side to side." Loughrey (1959:40) observed further that the abrasion pattern "seems to indicate that [the walrus] . . . ploughs or scrapes the bottom with its tusks by a sideways and forward thrusting motion of the head." He rejected as untenable Johansen's (1912) report of the animals moving "backward" and raking the bottom with their tusks, for he observed that the posterior surfaces were not abraded in accord with that procedure. My findings also offer no support for the digging and raking hypothesis.

Close inspection of the surfaces of the tusks has revealed that the direction of movement of the majority of abrasive particles is from proximal to distal, as would occur if the animal moved forward along the bottom, dragging its tusks in the sediments. This pattern is consistent also with that of abrasion on the vibrissae. Furthermore, the site of maximum abrasion of the tusks is on the anteriormost arc, which in adults usually is some distance away from the tips and on a plane with the front of the snout. The position of the tips relative to that plane seems to determine their rate of linear decrement, for the highest rates occur in young animals, in which the tips extend to or beyond the rostral plane. Thereafter, as the tusks increase in length and begin to recurve, the brunt of the abrasive force is taken up on the shafts, rather than the tips, and the rate of linear decrement diminishes. This probably is the explanation for the lower rate of decrement in females than in males, for the tusks of females tend to be more strongly arched than those of males; hence their tips should be less affected.

Evidence of side-to-side motion, as hypothesized by Mansfield (1958*a*), was absent on the specimens that I examined. Virtually all of the signs of abrasion indicated forward motion of the animal, with tusks and snout pressed against the bottom. The characteristics of the skin on the face, the abraded surfaces of the vibrissae, and the abrasion on the tusks all indicated to me that digging, if done at all, is accomplished by "rooting" with the upper edge of the snout, rather than with the tusks.

Relation to Social Behavior

The primary role of the tusks probably is a social one. The importance of tusks, horns, antlers, and other such appendages as signals of social rank in terrestrial mammals has been recognized in a general way for a long time and confirmed by several detailed studies (Verheyen 1954; Espmark 1964; Geist 1971). Although such appendages often function secondarily as weapons, their primary value is in ritualized dominance-threat displays in which fighting per se is minimized and often amounts to no more than a show of strength (Carthy and Ebling 1964:3; Geist 1966; Miller 1975*a*). The evolutionary impetus leading to enlargement of such structures is now recognized as self-reinforcing; the success of the bearer in establishing his dominance during mating is reflected in his greater contribution to the gene pool (Bartholomew 1970). The individual that lacks those social appendages may survive and even prosper, but he probably will not be able to mate.

The walrus' use of its tusks in threat displays (Frontispiece) was formally reported first by Loughrey (1959:48), who observed that an animal with very large tusks can intimidate others "to move out of its way simply by threatening them," whereas one with smaller tusks is met with active opposition from his peers. Both large tusks and large body size exert positive influence on achievement of a socially dominant position in male walruses (Miller 1975*a*), and I feel certain that the same is true in females, on the basis of my own general observations.

The real test of social importance of the walrus' tusks probably will be derived from analysis of the behavior of adult males in the mating season, for it is in the competition for mates that such organs, whether epigamic or rank-symbols (or both), play their primary role and have the greatest immediate and long-term impact on the gene pool (Bartholomew 1970; Geist 1971; Miller 1975*a*).

For the females, the information now available does not show any clear indications of specific seasons or activities in which social or other functions of the tusks are paramount. By analogy with other mammals in which appendages of this kind are present in both sexes, I presume that the maximum social value of the female's tusks is in competition for some resource that is important for survival of the young or for maintaining the ability to reproduce (cf. Henshaw 1969). That they do function as rank symbols in the minor day-to-day contests within the herd is apparent, but it is not yet clear how important the outcome of those conflicts (mainly for space on the haulout) may be to the individual female or her calf.

Other Functions

Ancillary functions of the tusks include their use as weapons, both offensively and defensively. This has been reported many times, mainly in anecdotal accounts of the animals' attacks on hunters and their boats (e.g., Lamont 1861:85,138; Hayes 1867:404–411). These attacks appeared to be mainly by females in defense of their young, although the interpretations are open to question. Many similar incidents have been reported to me and to others (e.g., Vibe 1950:49) by the Eskimos. In most of those reports, however, the aggressors were juveniles and subadults, rather than adults (see Brooks 1954:71).

Use of the tusks as auxiliary appendages for locomotion, especially when hauling out on ice or land, also has been recognized for a long time (Allen 1880:137) and was the basis for the generic name *Odobenus* (Greek: *odus*, *odonto* = tooth; *baeno* = walk). Their use in this way is common and is, I believe, one of the principal causes of fracture of tusks, especially when the animals haul out on rocky islets.

I have observed that the tusks also are used occasionally in other ways, some examples of which are as follows:

- A female and calf on the ice were approached by a party of hunters, who attempted to kill the female but succeeded only in wounding her. She dove into the water, leaving the calf behind, and the latter was promptly captured alive by the hunters. The wounded female then surfaced about 15 m away in an area of gray ice about 15 cm thick. Sighting the calf and the hunters, she immediately began chopping her way toward the group by vigorously thrusting her tusks downward, breaking the ice before her. She continued until she reached the floe where the calf was located.
- A subadult female lay at the edge of a small floe on which several other walruses were sleeping. She gazed first at the other animals, then at the water, then began chopping at the ice near her with her tusks. After chopping away some 3 to 5 kg of the edge of the floe, she rolled off into the water and swam away.
- An adult female surfaced in a round hole in ice that was about 20 cm thick. The hole was only large enough for her head and neck. Immediately, she began to abrade away the ice around her by pressing the shafts of her tusks against the edges of the hole and swinging her head rapidly from side to side. This behavior was similar to "ice-sawing" by Weddell seals (*Leptonychotes weddelli*) and appeared to serve the same purpose.
- On numerous occasions, I have seen walruses resting or sleeping in the water with their tusks hooked over the edge of the ice, their body lying either horizontally or vertically in the water. The tusks appeared to function both as a prop for the head, keeping the mouth and nostrils out of the water, and as an "anchor" preventing the animal from drifting away with the current.

Clearly, the tusks are used in many ways in addition to their apparently primary function as social organs, but none of these as yet has been linked with feeding. Their use in chopping and abrading ice has not been reported before, although the Eskimos have been aware of this function for a long time. Use of the tusks in these ways for creating and maintaining holes in the ice could be their most important secondary function. Maintenance of access between air and water is vital for survival, especially in wintering areas where leads and polynyas often are scarce.

Positive selective pressures and the potential for tusk development probably have existed in all polygynous pinnipeds from the beginning. All but the late Miocene to Recent odobenids, however, are (or were) piscivorous. Piscivory requires a long gape that allows full use of the battery of pointed teeth for capture of fast-moving prey. Obstruction of that gape by huge, laterally placed tusks is disadvantageous in piscivory, hence evolutionary development of tusks in piscivorous mammals probably tends to be prevented by strong negatively selective pressures. With benthic feeding, however, only the anterior end of the mouth needs to be kept free from such obstructions; the integrity of the rest of the gape becomes less important. This should tend to lessen the negative selection and permit the positive pressures for tusk development to override them. The odobenids' change from pelagic–piscivorous (much like present-day sea lions) to benthic-molluscivorous feeding apparently took place in the Miocene epoch, before walruses made the transit from Pacific to Atlantic. At the time of their passage through the Central American Seaway in the Pliocene epoch, walruses already had enlarged, tusk-like canines (Repenning 1976; Repenning and

Tedford 1977). It is my contention that it was the change in feeding habits from piscivory to molluscivory which enabled the positive pressures of social advantage to prevail and allowed the upper canines to evolve as tusks.

Food and Feeding Behavior

To the Eskimos and other coastal people of the Arctic, the fact that walruses feed mainly on bivalve mollusks has been common knowledge, probably for thousands of years. Documentation of that fact in the scientific literature was meager until the present century, when Chapskii (1936), Tsalkin (1937), Vibe (1950), Mansfield (1958*a*), and Loughrey (1959) reported their findings from the North Atlantic region, and Nikulin (1941), Freiman (1941), Brooks (1954), Krylov (1971), and Fay et al. (1977) presented comparable information from the Bering and Chukchi seas. The information in most of those reports is only qualitative, consisting of identifications of the kinds of organisms found in stomach contents of walruses and estimates of relative importance of each class of prey, based on the number of genera represented. Quantitative details of actual numbers and weights of prey were presented principally by Vibe (1950) and Fay et al. (1977), who compared their findings with faunal information from benthic sampling, in efforts to evaluate the impact of the walrus' feeding on the food resources available.

Some additional information on kinds and quantities of prey consumed was obtained in the present study. My primary objective, however, was to answer other questions which would contribute to understanding of the feeding behavior and energetics of walruses:

- How long is the calf dependent on its mother for milk?
- What quantities and qualities of milk are required?
- When does the young walrus begin to feed on benthic invertebrates?
- Where do those invertebrates reside and under what conditions?
- How does the walrus locate, identify, and ingest them?
- What quantities and qualities of prey does it require for sustenance?
- Do those requirements differ seasonally, geographically, or in relation to major biological events, such as mating and molting?

The following account mainly addresses those questions.

Diet of Calves and Other Young Animals

Length of the Suckling Period

The young walrus ordinarily stays with its mother for about 2 years (Chapskii 1936). After that time, young males may stay for 2 or 3 years longer with the adult females before joining all-male herds; the young females tend to stay with the adult females continuously. From examination of stomach contents, Chapskii (1936), Freiman (1941), Nikulin (1941), Brooks (1954), Mansfield (1958*a*), and Loughrey (1959) concluded that young walruses probably are dependent entirely on the mother's milk for at least the first year after birth, and that they gradually are weaned during the second year.

I found the stomachs of calves less than 1 month old to be either empty or filled with milk. The St. Lawrence Islanders also stated that they never found anything other than milk in the stomach of newborn calves taken during April to June. Two of 60 hunters contacted stated that they occasionally had found bits of solid food (invertebrates) in stomachs of 5- to 6-month-old calves taken in November and December. From the infrequency of such reports, I judge that the calves do not take solid foods very often at that age. A calf born in captivity at Marineland voluntarily began to take solids in small quantities when about 8 months old (T. Otten, personal communication).

On one occasion in March, I watched about 20 calves (about 10 months old) that were diving with their mothers while the latter apparently were feeding (based on their repeated dives in the same location and their bringing up invertebrates in their mouth), but I was unable to determine whether the calves also were feeding on benthos. In two of three 12- to 13-month-old animals, I found only milk, but the third contained an operculum of *Neptunea* sp. (a large gastropod mollusk), along with some stones and gravel (Table 19). E. H. Miller and B. Hines (personal communication) reported the presence of a calf about 13 months old at Round Island in 1972. That animal, unaccompanied by its mother, was fat and seemed in normal health (Fig. 95), suggesting that it had been feeding independently.

Table 19. *Stomach contents of young walruses less than 3 years old.*

		Number of stomachs containing			
Age (months)	Number examined	Milk only or empty	Milk and invertebrates	Invertebrates only	Authority[a]
0–1	10	10	0	0	M, U
2–3	> 3	> 3	0	0	F, M
4–5	3	3	0	0	C, M
6–7	>20	>20	few	0	G
12–13	3	2	0	1	U
14–15	9	7	0	2	B, C, M, N, U
16–17	10	10	0	0	C, L, M
17–18	<10	most	few	few	G
22	1	0	1	0	U
24–27	>11	2	1	>8	B, C, F, G, L, M, N, U

[a] B = Brooks (1954), C = Chapskii (1936), F = Freiman (1941), G = Gambell Eskimos (personal communication), L = Loughrey (1959), M = Mansfield (1958*a*), N = Nikulin (1941), U = F. H. Fay (unpublished data).

In seven out of nine animals that were 14 to 15 months old, the stomach contained only milk or was empty. In the stomach of one of this age reported by Brooks (1954:59), however, there were "stones and animal matter"; in the stomach of another that I examined, there were about 10 kg of feet of the bivalve *Serripes groenlandicus*. Because each of these latter two animals was alone, rather than accompanied by an adult, the stomach contents may have been atypical for animals of their age. Nevertheless, they indicated that some

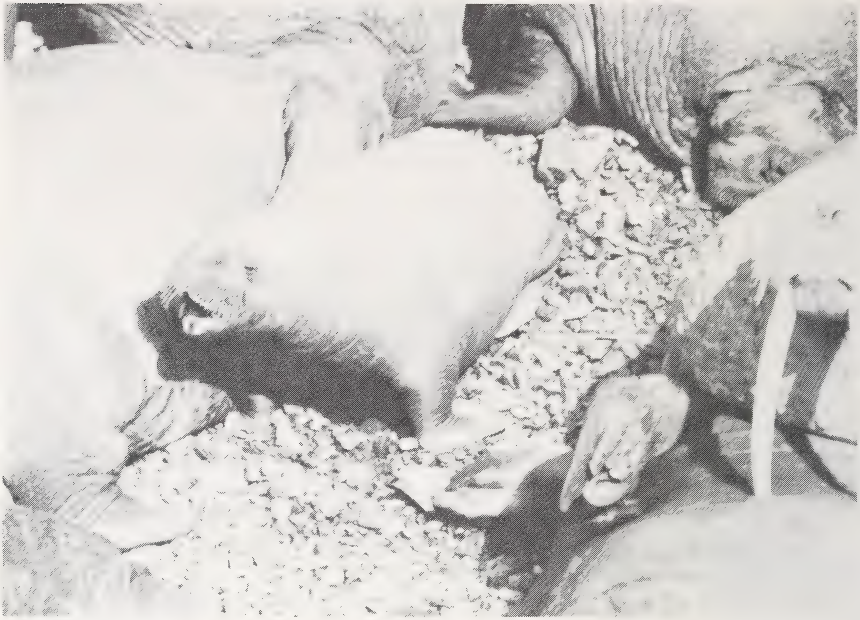


Fig. 95. Calf, about 13 months old, in a herd of adult males at Round Island, Bristol Bay in June 1972. (Photo by B. Hines)

individuals of this age are capable of feeding on benthic invertebrates.

According to the St. Lawrence Islanders, the 17- to 18-month-old young accompanied by an adult usually have only milk in the stomach, but some contain both milk and invertebrates; a few have only invertebrates. Although I was not able to confirm this, I examined the stomach of a 22-month-old animal, which contained a mixture of milk and soft-shelled (molting) brachyuran crabs of the genus *Chionoecetes*.

Two 24-month-old animals that I examined had only benthic invertebrates in their stomachs, as did several examined by Chapskii (1936), Brooks (1954), Mansfield (1958*a*), and Loughrey (1959). However, Nikulin (1941) and Freiman (1941) found one 26- to 27-month-old animal that had only milk in its stomach and another that had both milk and mollusks.

On two occasions, I observed 34- and 35-month-old animals suckling. Since the adults that they were with had no other younger animals with them, I assume that both of these were parent–offspring pairs that had remained together longer than the usual 2-year period.

In summary, the data available suggest that (1) calves are dependent on milk alone in at least the first 5 months after birth, (2) some calves may begin to eat invertebrates infrequently by the time they are 6 months old, (3) a few are proficient at benthic feeding by the end of their first year, but (4) they usually continue to suckle, at least as a dietary supplement, for several months longer, (5) their milk intake probably declines radically toward the end of the second year, (6) they usually are fully weaned at 2 years of age, but (7) a few may continue to suckle for another year if not supplanted by a younger, more dependent calf.

Composition of Walrus Milk

I collected four samples of milk from walruses taken in May 1958. The first three samples were obtained by severing the lactiferous duct beneath the skin and catching the milk in a sterile container. The fourth sample was taken from the stomach of a calf (about 1 week old) that had been suckling immediately before it was killed. I collected one comparative sample from the stomach of a 2-to 3-week-old bearded seal (*Erignathus barbatus*); three samples from adult northern fur seals were supplied by R. S. Peterson and E. T. Lyons from females that were 1 h prepartum, 36 h postpartum, and about 10 days postpartum (Table 20, Samples I, II, and III, respectively).

A pinch of powdered bichloride of mercury was added to each sample at the time of collection and thoroughly mixed with it to inhibit fermentation of any sugars present. After collection, the samples were cooled to 0 ± 2°C and stored at that temperature for about 2 weeks. The samples were analyzed by H. F. Meyers and M. Arnow of the Sanitation Chemistry Laboratory, Arctic Health Research Center, Anchorage, Alaska.

The analytical results (Table 20) indicate that in gross composition the milk of walruses resembles that of other pinnipeds in having very high fat and protein contents, low water content, and very low or no reducing sugars (cf. Sivertsen

Table 20. *Gross composition of walrus milk, with comparative analyses of milk from other pinnipeds.*

		Composition (% by weight)[a]				
Sample	Volume (mL)	Water	Fat	Protein	Sugar	Ash
Walrus						
I	10	67.6	13.8	–	–	0.63
II	25	54.0	31.6	11.0	–	0.47
III	30	61.5	26.9	7.3	<0.025[b]	0.75
IV	50	56.5	32.0	5.0	<0.025[b]	0.55
Bearded seal						
I	50	46.4	49.5	6.8	0.05	0.60
Fur seal						
I	30	28.1	59.1	15.6	0.02	0.36
II	30	33.1	54.1	17.5	0.016	0.41
III	30	36.6	49.5	13.5	0.022	0.60

[a] Analyses: water, ash, fat by methods adopted by Association of Official Agricultural Chemists (Horowitz 1955); protein (nitrogen) by modified AOAC methods, using Hengar selenized granules instead of mercury and collecting distillate in boric acid for direct titration; sugar (reducing substances) by ether extraction of fat, followed by protein precipitatoin by Folin-Wu method (Hawk et al. 1947:493) and Benedict's method applied to filtrate. Composition data are means of replicate analyses (two each), except for Walruses I and II.

[b] No sugars detected to the 0.025% level; not analyzed for smaller amounts.

1941; Amoroso et al. 1951; Rand 1956; Pilson and Kelly 1962; Ashworth et al. 1966; Kerry and Messer 1968). The relative amount of each fraction varied among samples, possibly in relation to the stage of lactation (Bryden 1968; Van Horn and Baker 1971).

The water content of the walrus milk tended to be somewhat greater and the fat content somewhat less than in milk from the other pinnipeds. The protein fraction was comparable in amount to that in milk of the bearded seal but was 30 to 50% lower than that of the fur seal. The carbohydrate content (if any) was not detectable by the method used on the walrus samples. Absence of lactose in walrus milk was reported earlier by Pilson (1965) and confirmed by Herber and Peterson (*in* Kerry and Messer 1968). Those investigators also determined that the enzymes necessary for hydrolysis of milk disaccharides, such as lactose, are absent or occur only in trace amounts in the intestine of the walrus calf.

The gross energy value of walrus milk, based on the mean composition of samples II, III, and IV of Table 20 and on the standard caloric values for milk constituents (from Kleiber, 1961:312), is about 3,240 kcal/L.

The low fat content of walrus milk may account for the low rate of postnatal weight increase in walrus calves, compared with phocid pups (cf. Laws 1953*b*; Mansfield 1958*b*; McLaren 1958). Nevertheless, its fat content is very high relative to the milk of most terrestrial mammals, and its water and sugar contents are low. These are characteristics of all marine mammal milks, and they seem clearly adaptive to life in the sea, where fresh water is scarce and there is a high demand for metabolic heat (Irving 1968; Depocas et al. 1971). Fat is an efficient source of both heat and water for the calf, for it possesses more than twice the caloric value of lactose per unit volume and liberates large quantities of metabolic water when oxidized (Dukes 1955). Probably the low water and sugar contents are adaptive also for the lactating adult, for the synthesis of sugars requires much water, and water conservation probably is of critical importance, especially in the first days or weeks after parturition. At that time, the mother seems to do little or no feeding. Of 46 cows with newborn calves that I examined, only 3 (6%) had any food in the stomach, and the amount in those 3 was not more than a handful. Conversely, 31 of 89 (35%) other animals taken in the same area, at the same time, had food in the stomach, and in most of them this amounted to several kilograms.

Rate of Intake of Milk

The frequency of feeding and volume of milk consumed by walrus calves under natural conditions have not been determined, but there is a substantial amount of data on this subject from calves reared successfully in captivity. Those data may be indicative of the feeding rate under natural conditions. I obtained information on milk intake from records of 12 walrus calves that were reared in the Copenhagen Zoological Garden (Reventlow 1951), the San Diego Zoological Garden (Pournelle 1961), Marineland of the Pacific (Brown and Asper 1966; D. H. Brown, personal communication), and the New York Aquarium (G. C. Ray, personal communication). In each instance, the calves gained weight during the first 4 to 9 months at rates ranging from 0.27 to 0.59 kg per day (mean, 0.42 kg per day); their body weight doubled in about 6 months.

Each of these calves was reared on a diet of artificial marine mammalian milk, which was provided to them in two to four allotments per day. Since they were not fed ad libitum, there is some justification for doubt that their rate of intake was as high as it might have been under less restrictive conditions. From my experiences in the first weeks of rearing seven of those calves, and from subsequent, detailed reports on their treatment (D. H. Brown, G. H. Pournelle, and G. C. Ray, personal communication), however, I am confident that the volume of milk consumed in any 24-h period was governed more by the calves than by their keepers. The calves often were unable or unwilling to accept all of the milk that was made available to them. Because the rate of intake of food by mammals tends to be a function of their nutritional requirements, rather than of the capacity of their digestive tract (Kleiber, 1961:284–285), I assume that the amounts ingested usually were governed by the individual's needs.

The artificial milk that each animal received was mainly a mixture of heavy cream, minced clams or fishes, and fresh water, in proportions of about 4:5:3, with supplementary vitamins. Although the components were somewhat different in each instance, the nutritive qualities were about the same, judging from the comparable growth of the animals. The gross composition of the artificial milk was different from that of natural walrus milk, having about 60% less fat, 30% more water, and more than 100 times more carbohydrate, but a similar protein content (Table 21). The gross energy value of this mixture per unit volume was about 50% that of natural walrus milk.

Table 21. *Approximate gross composition and energy value of artificial marine mammal milks on which walrus calves were reared in captivity.*

	Percentage composition[a]				
Location	Water	Fat	Protein	Sugars	Energy value (kcal/L)[b]
Marineland of Pacific	73.4	12.7	10.3	2.4	1,860
New York Aquarium	78.7	10.6	6.6	2.8	1,480

[a] Based on formulae for liquid diets provided by Brown and Asper (1966) and G. C. Ray (personal communication) and on the composition of their constituents, as given by Spector (1956:190).

[b] Based on the energy values of milk constituents, as given by Kleiber (1961:312).

The rate of intake of artificial milk was about 3 to 6 L per day in the first month, increasing to 13 to 15 L per day in the eighth month (Table 22). Expressed as a function of total body weight (TBW), this amounted to an intake by weight (17 observations) of 6.5 to 9.3% TBW per day (mean, 9.2%), which was a large amount, but about 75% of it was water. The gross energy value of this diet amounted to about 135 kcal/kg TBW per day (60 kcal/lb per day), or about 20% more than the daily gross energy requirement of human infants on a diet of mother's milk (50 kcal/lb per day: Ebbs 1966). Expressed in terms of metabolic body weight (MBW = TBW $kg^{3/4}$: Kleiber 1961:209), the walrus calves consumed about 250 to 610 $kcal/kg^{3/4}$ per day (mean, 423 kcal), which was about 20% higher than the maximum rate of intake by domestic animals (253 to 452 $kcal/kg^{3/4}$ per day; mean, 351 kcal: Kleiber 1961:319). These differences

Table 22. *Estimated mean daily intake of artificial walrus milk, in relation to body weight, of walrus calves reared in captivity.*

Age (months)	Total body wt (kg)	Milk per day		Gross energy (kcal per day)		Source[b]
		Liters	% TBW[a]	Total	Per kg$^{3/4}$ of TBW	
1	46	3	6.5	4,440	251	R
1	54	4.2	7.8	7,812	393	BA
1	56	4.7	8.3	8,742	462	BA
1	63	4.7	7.4	8,742	390	BA
1[c]	66	5.7	8.6	8,436	364	P
1	70	4.7	6.7	8,742	361	BA
2	62	5.4	8.7	7,992	362	Ra
4	90	7	7.8	10,360	355	R
4[c]	127	10.9	8.7	16,132	427	Ra
8	154	14.3	9.3	26,598	609	BA
8	161	12.9	8.0	23,994	532	BA
8	170	14.9	8.8	27,714	590	BA
8	186	14.9	8.0	27,714	550	BA

[a] Percent of total body weight (TBW), assuming milk weight of 1 kg/L.

[b] BA = Brown and Asper (1966), P = Pournelle (1961), R = Reventlow (1951), Ra = G. C. Ray (personal communication).

[c] Three animals; data given as mean for group.

suggest that either the walrus calves had a higher caloric requirement than is normal for domestic animals, or they were not able to use their food very efficiently. The latter seems to me more probable, for the following reasons:

- The gross energy value per unit volume of the artificial milk was about half that of natural walrus milk, hence the calves probably had to ingest at least twice the volume that would have been required had they been feeding on natural milk.
- At that rate, the calves would have consumed about two-thirds as much fat, but more than twice as much protein and 200 times more carbohydrate than would have been available in the caloric equivalent volume of natural milk.
- At least half of that carbohydrate was lactose, which would not have been available to the calves as digestible energy, because of their lack of lactase.
- Much of the protein also may have been unused, if it were greatly in excess of the normal (natural) rate of intake.

Thus it seems likely that the prepared diet was greatly unbalanced and that the net energy available from it was appreciably lower than would have been available from a caloric equivalent volume of natural walrus milk. The natural milk must be assumed to be optimally balanced, with very high net digestible energy, perhaps comparable to the 84% available to human infants on mother's milk (Ebbs 1966).

The daily net digestible energy intake by calves probably is comparable to that of young domestic mammals (about 350 kcal/kg TBW$^{3/4}$ per day). This intake of natural milk would amount to about 6.8% of the TBW per day. The rate of intake for walrus calves under natural conditions may be slightly higher because of the demands of thermoregulation in a cold environment (Fay and Ray 1968; Iversen and Krog 1973).

After the calves begin to take solid foods, their daily rate of intake of milk/kg TBW probably declines, but the volume ingested per day may increase for several months, as their body weight increases. The nutritional demands on the mother, during that period, undoubtedly are much higher than they would be for her own maintenance. In other mammals, lactating females may consume one to two times more food per day than do non-lactating animals of comparable size (Brody 1945; Kleiber 1961).

Diet After Weaning

The principal foods eaten by walruses (other than by suckling calves) are mollusks, mainly the bivalves *Mya truncata*, *Astarte borealis*, *Serripes groenlandicus* (= *Cardium groenlandicum*), and *Hiatella arctica* (= *Saxicava arctica*) (Johansen 1912; Tsalkin 1937; Nikulin 1941; Vibe 1950; Brooks 1954; Mansfield 1958*a*; Loughrey 1959). In the past there has been some debate over the presumed herbivorous habits of walruses (Allen 1880). More recent observations by several investigators have established that marine vegetation is not an important part of the diet, though it may be ingested incidentally in small amounts. Many kinds of benthic invertebrates and even a few vertebrates are eaten. None other than mollusks appear to be of more than secondary or tertiary importance by volume, but some prey that are taken in small quantities may be of critical importance because they contain needed trace elements or other nutrients that are scarce or absent in mollusks.

Kinds of Prey

More than 60 genera of marine organisms, representing 10 phyla, have been identified as prey of the Pacific walrus (Table 23). A few examples from each phylum will be discussed here, in regard to their distribution, habitat, and relative abundance, based on Ricketts and Calvin (1948), MacGinitie and MacGinitie (1949), Pavlovskii (1955), Filatova (1957), MacGinitie (1959), Savilov (1961), Sparks and Pereyra (1966), and Petersen (1978). The purpose of this description is to illustrate the wide variety of life forms eaten by the Pacific walrus and to provide a basis for consideration of the kind of effort required of the walrus to obtain them.

Coelenterata.—The soft coral *Eunephthya rubiformis* (Fig. 96*a*) is a tough, sessile colony of rosy to translucent polyps, usually 3 to 7 cm in diameter when retracted. It attaches to stones or molluscan shells on the sea bottom at depths from less than 10 to more than 200 m and is widely distributed in the Bering and Chukchi seas. I have found it frequently in beach windrows on western St. Lawrence Island, which suggests that it is abundant there, near shore. *E. rubiformis* was present in only 1 of 51 walrus stomachs that I examined from that area, but I found fragments of it in feces from several other individuals in the same locality.

Annelida.—At least five genera of polychaetes have been identified as prey of the Pacific walrus. These include both predaceous and detritophagus forms that reside in tubes or burrows in the surface layers of sediments at water depths from

Table 23. *Systematic list of organisms that have been identified as foods of the Pacific walrus.*[a]

Organism	Authority[b]
Phylum COELENTERATA	
Class Anthozoa	
Actinarian (cf. *Metridium* sp.)	Fa
Eunephthya rubiformis (Pallas)	U
Phylum ANNELIDA	
Class Polychaeta	
Lumbrinereis sp.	Fa
Nephthys sp.	N, B, Fa
Onuphis conchylega M. Sars	K
Maldane sarsi Malmgren	N
Pectinaria sp.	Fa
Phylum SIPUNCULIDA	
Golfingia margaritacea (M. Sars)	Fa
Unidentified (probably *Golfingia*)	B
Phylum ECHIURIDA	
Echiurus echiurus Pallas	N, K, Fa
Phylum PRIAPULIDA	
Priapulus caudatus Lamarck	N, B, K, TK, Fa
Phylum MOLLUSCA	
Class Gastropoda	
Solariella sp.	N
Margarites sp.	K, Fa
Natica clausa Broderip & Sowerby	N
Natica sp.	Fa
Polinices sp.	Fa
Buccinum sp.	N, Fa
Neptunea (= *Chrysodomus*) sp.	N, B, Fa
Velutina sp.	U
Nudibranchia unidentified	Fa
Class Bivalvia	
Musculus sp.	U
Nucula tenuis (Montagu)	N, K, Fa
Astarte borealis (Chemnitz)	N, Fa
Astarte sp.	B
Cyclocardia (= *Cardita*) cf. *ventricosa* (Gould)	U
Thyasira flexuosa (Philippi)	K
Clinocardium nuttallii (Conrad)	B
Clinocardium cf. *ciliatum* (Fabricius)	Fa
Serripes groenlandicus (Chemnitz)	N, Fa
Liocyma viridis Dall	U
Tellina lutea Gray	Fa
Yoldia hyperborea (Loven)	K, Fa
Macoma calcarea (Chemnitz)	N, B, K, U
Mactra sp.	K
Spisula polynyma (Stimpson)	Fa
Mya truncata Linnaeus	N, B, K, TK, Fa
Mya cf. *pseudoarenaria* Schlesch	Fa

Table 23. Continued

Organism	Authority[b]
Hiatella (= *Saxicava*) *arctica* (Linnaeus)	N, B, Fa
Hiatella striata (= *S. rugosa*) (Fleuriau de Bellevue)	N
Class Cephalopoda	
Octopus californicus (Berry)	K
Octopus sp.	Fa
Benthoctopus (= *Polypus*) sp.	N
Phylum ARTHROPODA	
Class Crustacea	
Balanus sp.	Fa
Mysidae unidentified	K
Anonyx nugax (Phipps)	Fa
Ampelisca macrocephala Lilljeborg	TK, Fa
Hippomedon sp.	Fa
Lembos sp.	Fa
Gammaridae unidentified	K
Hyppolytidae unidentified	K
Caridean unidentified	Fa
Pandalus sp.	K
Argis (= *Nectocrangon*) *lar* (Owen)	K, Fa
Sclerocrangon boreas (Phipps)	B, Fa
Pagurus trigonocheirus (Stimpson)	Fa
Chionoecetes opilio (Fabricius)	N, K, Fa
Hyas coarctatus alutaceus Brandt	B, K, Fa
Paralithodes camtschatica (Tilesius)	T
Brachyuran unidentified	Fa
Phylum ECHINODERMATA	
Class Holothuroidea	
Thyonidium commune	Fa
Psolus sp.	Fa
Cucumaria sp.	N, K, Fa
Molpadia arctica (v. Marenzeller)	B
Phylum UROCHORDATA	
Boltenia ovifera (Linnaeus)	U
Pelonaia corrugata Goodsir & Forbes	N, K, Fa
Tethyum aurantium (Pallas)	K
Tethyum sp.	Fa
Phylum VERTEBRATA	
Class Teleostomi	
Lumpenidae (= Stichaeidae) unidentified	K
Blenniidae (= Pholidae) unidentified	K
Class Mammalia	
Erignathus barbatus (Erxleben)	B, Fa, LF
Phoca hispida (Schreber)	N, B, K, S, LF
Phoca largha Pallas	S, LF

[a] Invertebrate classification follows Barnes (1968).

[b] N = Nikulin (1941), B = Brooks (1954), T = Tikhomirov (1964), S = Shustov (1969), K = Krylov (1971), TK = Tomilin and Kibal'chich (1975), Fa = Fay et al. (1977), LF = L. F. Lowry and K. J. Frost (unpublished data), U = F. H. Fay (unpublished data).

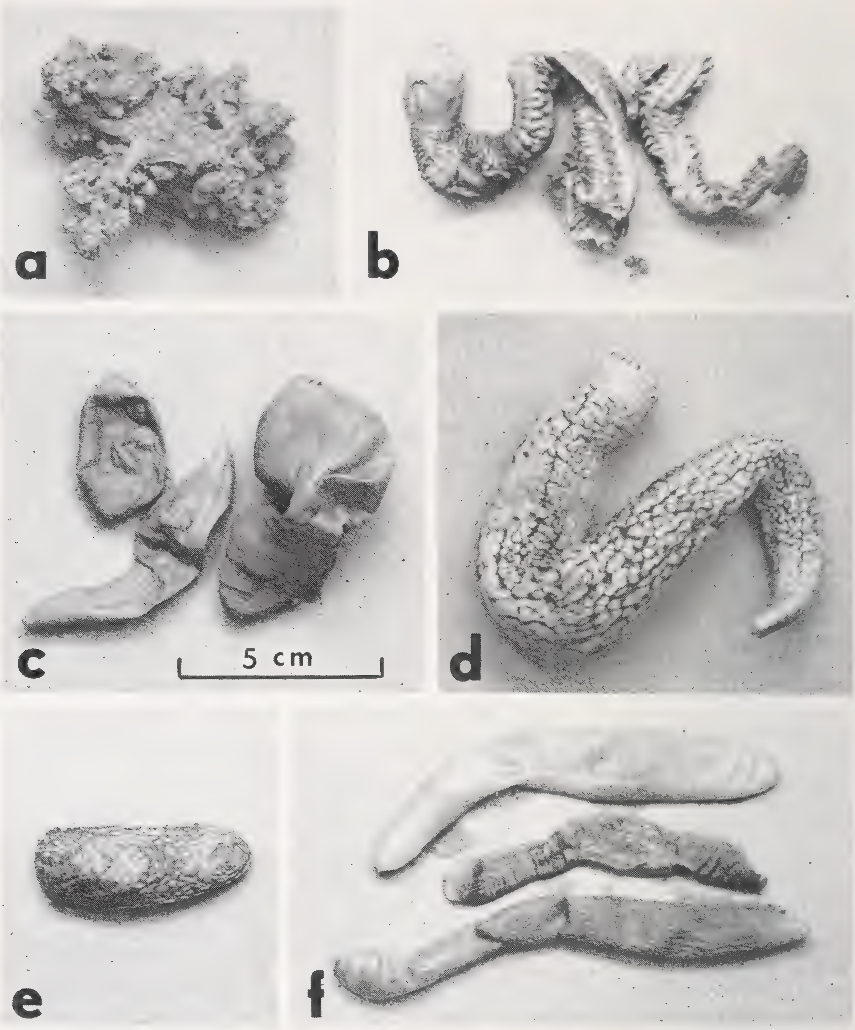


Fig. 96. Examples of six kinds of benthic invertebrates taken from stomachs of Pacific walruses: (a) *Eunephthya rubiformis*; (b) *Nephthys* sp.; (c) *Echiurus echiurus*; (d) *Thyonidium commune*; (e) *Psolus* sp.; and (f) *Pelonaia corrugata*. (Photos by F. H. Fay)

about 20 m to more than 100 m. They usually occur in small numbers in the stomach contents, but large individuals of *Nephthys* sp. (Fig. 96*b*) may make up the greatest part of the ingesta.

Sipunculida.—The large sipunculid worm (to 23.5 cm) *Golfingia margaritacea* (Fig. 97*a*) is a common inhabitant of sandy sediments in the Bering and Chukchi seas at depths from the littoral zone to more than 300 m, where it resides in a shallow burrow. This species occurs commonly in stomachs of walruses taken in the Bering Strait area in spring, but usually in small numbers.

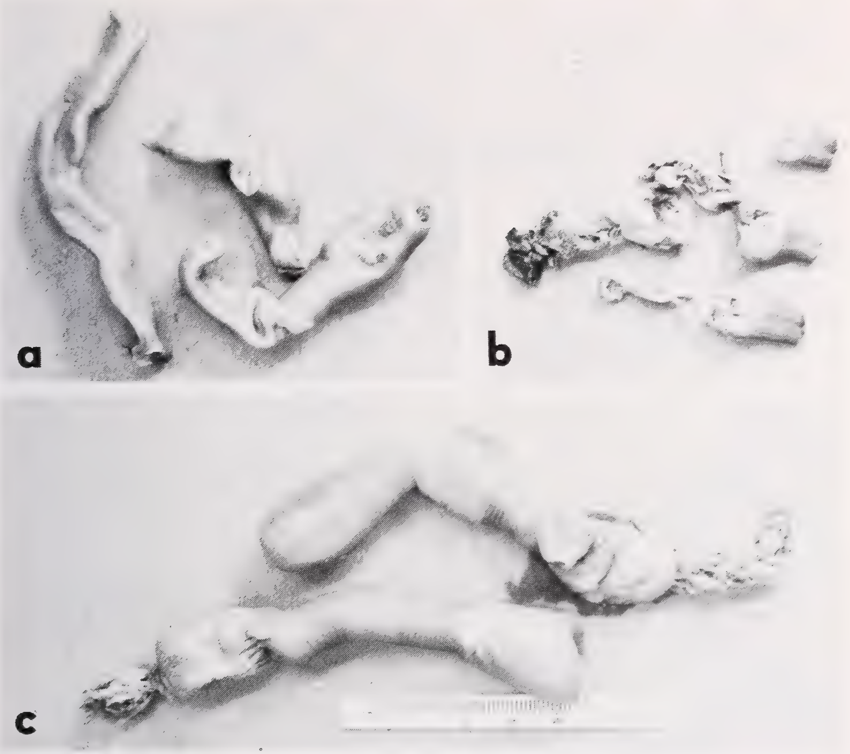


Fig. 97. Three kinds of benthic invertebrates commonly found in stomachs of Pacific walruses: (a) *Golfingia margaritacea*; (b) siphons of *Hiatella arctica*; and (c) *Priapulus caudatus*. Scale in centimeters. (Photos by F. H. Fay)

Echiurida.—One of the invertebrates most often found in the ingesta of walruses in the Bering Sea is the nonsegmented worm *Echiurus echiurus* (Fig. 96*c*). Because of its delicate structure, it seldom is found intact in the alimentary tract but very often is indicated there and in the feces by the presence of its distinctively hooked, gold-colored setae. In the feces of bulls at Round Island in June, these setae were nearly the only organismal remains found, suggesting that *Echiurus* is a major prey item in that area, at that time. S. W. Stoker and I found it to be one of the three or four most common items in the feces of adult cows and subadults in the St. Lawrence concentration area during March, April, and May. This worm, up to 15 cm long and about 2 cm in diameter, resides in a shallow, U-shaped burrow in the mud. It seems to be very abundant and widely distributed in the Bering and Chukchi seas, at depths from the littoral zone to at least 80 m.

Priapulida.—A single species, *Priapulus caudatus*, of this phylum of nonsegmented worms is found in the Bering and Chukchi seas, where it inhabits silty bottom types at water depths from 5 m to at least 50 m. Like the worms mentioned above, *Priapulus* is a burrower in the upper layers of bottom

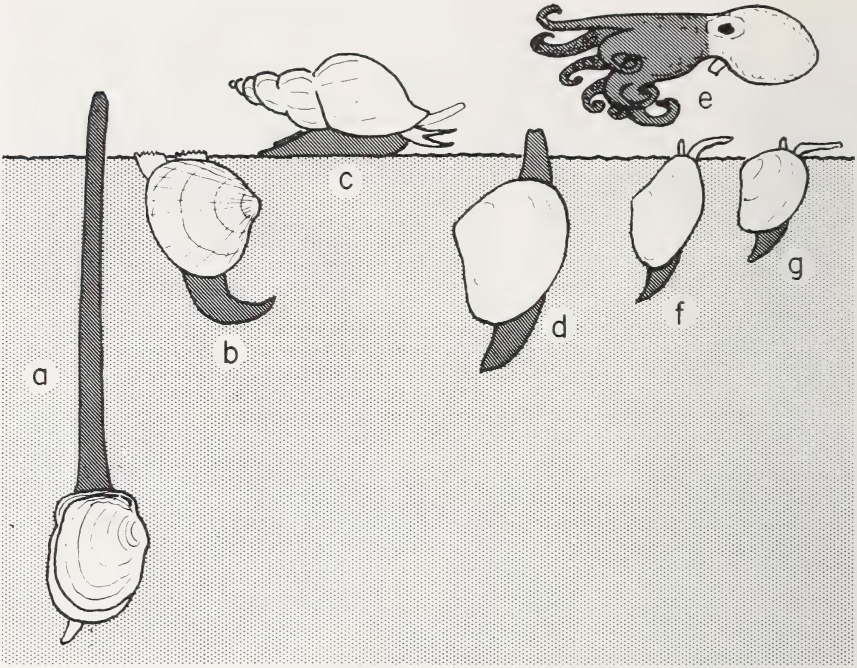


Fig. 98. Location in life of some of the mollusks eaten by walruses: (a) *Mya truncata*; (b) *Clinocardium ciliatum*; (c) *Buccinum* sp.; (d) *Spisula polynyma*; (e) *Octopus californicus*; (f) *Tellina lutea*; and (g) *Macoma calcarea*. Stippled area is vertical section of the bottom sediments to about 25 cm. Heavy shading indicates the parts of each organism usually found in the walrus' stomach. (b and g after Savilov 1961; e after Pavlovskii 1955)

sediments, where it feeds mainly on detritus. Large adults may exceed 15 cm in length and 2 cm in diameter (Fig. 97*c*). This organism occurs often in the feces and stomach contents of walruses, but usually as only one or two specimens per stomach.

Mollusca.—Bivalve mollusks (clams and mussels) have been found more often and in greater quantities than any other class of benthic invertebrates in the stomachs examined thus far. These comprised at least 15 genera, most of which are relatively large, long-lived organisms that make up about a third to a half of the total biomass of benthos on the intercontinental shelf of the Bering and Chukchi seas (Zenkevitch 1963; Stoker 1973, 1978). Gastropods (snails) were represented by at least eight genera, some of which are predaceous and feed on other mollusks. Cephalopods (two genera) rarely were represented. Nearly all of these mollusks are known to live on or in the upper few centimeters of bottom sediments, rather than deep beneath the surface (Fig. 98). Only two genera (*Mya* and *Spisula*) may burrow to considerable depths (20–30 cm), although *Mya* seems to be most often nearer the surface (Petersen 1978).

Very few of the mollusks represented in the stomachs examined thus far have been certainly identifiable to species, since the shell usually was absent. It is

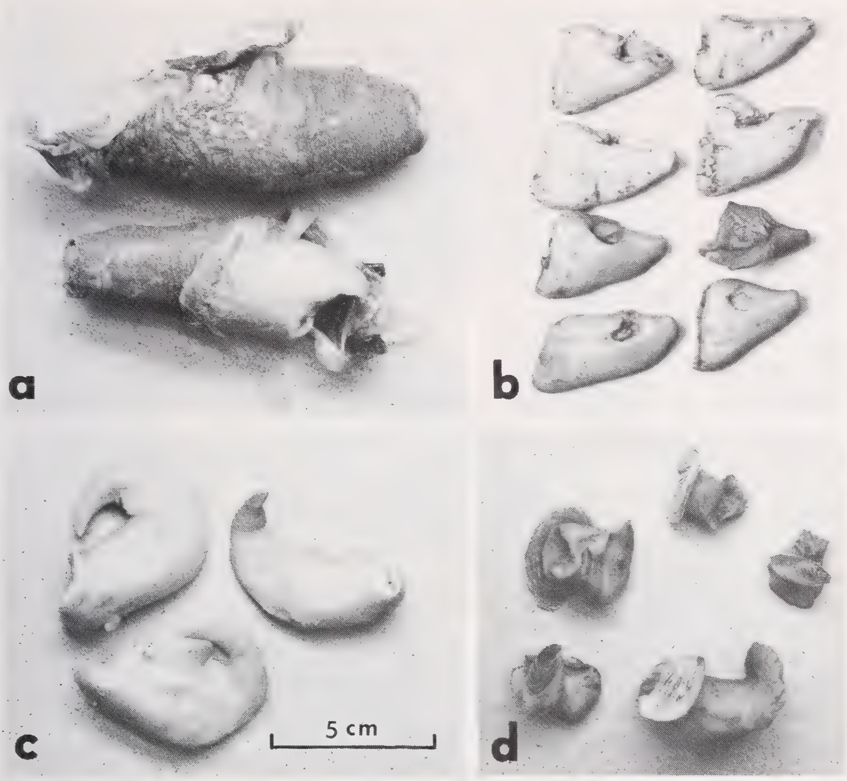


Fig. 99. Remains of mollusks from stomachs of Pacific walruses: (a) siphons of *Mya* sp.; (b) siphons of *Mya truncata*; (c) feet of *Serripes groenlandicus*; and (d) bodies of *Neptunea* spp. with operculae attached. (Photos by F. H. Fay)

usual to find only the foot or the siphon of bivalves (Figs. 97*b*, 99*a*,*b*,*c*) and the soft body of gastropods with the operculum attached (Fig. 99*d*). Only the tentacles of cephalopods have been found.

A few tiny mollusks up to 3 cm in diameter may be swallowed whole (*Margarites*, *Nucula*, *Cyclocardia*, and occasionally *Hiatella* and *Tellina*) with shells intact, but I have found only trace amounts of larger molluscan shells. The larger shells were represented by mere fragments, usually from the thin edges of the valves. Most frequently, these were from *Serripes groenlandicus*, the shell of which is rather fragile. That this scarcity of shells is not due to digestion was indicated by the fact that intact shells of small mollusks, as well as fragments from the valves of *S. groenlandicus*, were excreted in the feces, having passed through the entire digestive tract with remarkably little alteration. Some minute *Nucula*, *Margarites*, and *Cyclocardia* had both shells and soft parts virtually intact after passage through the tract.

Arthropoda.—About one-fourth of the walrus stomachs that I examined contained one or more crustaceans; in several instances, these were among the

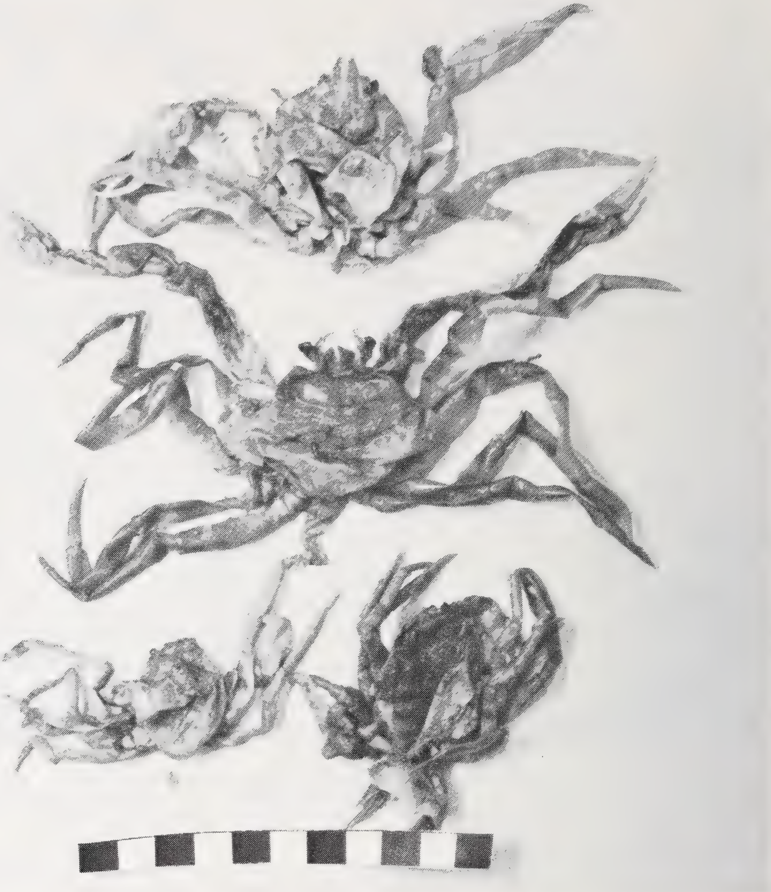


Fig. 100. Soft shelled (molting) crabs, *Hyas coarctatus*, from the stomach of a Pacific walrus. Scale in centimeters. (Photo by F. H. Fay)

two or three most common items in the ingesta. At least 15 genera of crustaceans have been found in the stomach contents of walruses taken in spring and summer in the Bering and Chukchi seas. These included mysids, amphipods, shrimps, pagurid (hermit) crabs, lithodid crabs, and brachyuran crabs. All of the represented genera reside on or in the uppermost strata of bottom sediments at water depths ranging from about 5 m to more than 1,000 m. All of the pagurid and brachyuran crabs that I found in walrus stomachs were in the soft-shelled stage of their molt (Fig. 100), suggesting that they are taken selectively, perhaps on a very seasonal basis.

Echinodermata.—At least five species of holothurians (sea cucumbers) have been found in the stomach contents of the Pacific walrus. Some of these occurred frequently enough and in large enough volume to indicate a high level of importance in the diet. Most common was the slender *Thyonidium commune*, about 15 cm long and 2 cm in diameter, which usually was found intact in the ingesta (Fig. 96*d*). Holothurians are mainly detritus feeders, living on or in the surface sediments at water depths ranging from the littoral zone to more than 1,000 m.

Urochordata.—Tunicates (sea squirts) of at least three genera were represented in the ingesta and feces of walruses in the St. Lawrence wintering area in north-central Bering Sea and in the Wrangell Island region of western Chukchi Sea. Most often and most abundantly represented in both areas was *Pelonaia corrugata* (Fig. 96*f*). One other, *Tethyum aurantium*, is said by the St. Lawrence Islanders to be common in the stomachs of walruses taken in autumn; another species, probably of this genus, was found occasionally in stomachs of walruses taken in both the St. Lawrence and Bristol Bay wintering areas. *P. corrugata* is sessile on the surface of soft to sandy bottom sediments at depths from the sublittoral zone to more than 100 m; *Tethyum* is an inhabitant of rocky areas, mainly at lesser depths.

Vertebrata.—The scarcity in walruses of endoparasites of known piscine origin indicates that fishes rarely are ingested (Deliamure 1955; Deliamure and Popov 1975). Only 2 of 240 stomachs from Pacific walruses that contained identifiable foods had remains of fishes. These were eight blennies in one specimen and two pricklebacks in the other (Krylov 1971). Although the arctic cod, *Boreogadus saida*, is known to be eaten by Atlantic walruses (Romer and Schaudin 1900 *in* Chapskii 1936; G. N. Safronova *in* Nikulin 1941; Pedersen 1962) and is abundant in the northern Bering and Chukchi seas, it has not yet been found in any stomachs of Pacific walruses.

Remains of two species of pinnipeds, the ringed seal (*Phoca hispida*) and bearded seal, consisting mainly of pieces of skin and blubber with some muscles and viscera, have been found with remarkable frequency (1 to 11%) in the ingesta and feces of Atlantic and Pacific walruses. Probably, most of these seals are taken as carrion, although it is conceivable that some are killed by the walruses (Fay 1960; Krylov 1971). L. F. Lowry and K. J. Frost (personal communication) found a walrus feeding on the carcass of a freshly killed spotted seal pup (*Phoca largha*); they found comparable remains of another pup nearby. Shustov (1969) reported the finding of spotted seal flesh in the stomach of a walrus.

Occurrence of the parasitic nematode *Trichinella spiralis* in 1 to 9% of walruses from various parts of the Arctic (see review by Rausch 1970) may be the result of their feeding on seals, especially bearded seals, for this is a parasite of carnivores in which transmission usually is accomplished by ingestion of the flesh of the prey by a predator.

Other ingesta.—In addition to the items classifiable as food, the digestive tract of the walrus usually contains a quantity of benthic sediments, apparently ingested incidentally. Such materials, ranging in size from fine sand to small stones, made up nearly 2% of the total volume of ingesta in the walruses examined by Fay et al. (1977), and varied in amount from a trace to 1.04 kg per stomach. Other inanimate items in the same stomachs included a small piece of seaweed (*Laminaria* sp.), a piece of broken glass, and a fragment of gasket material from an internal combustion engine.

Seasonal and Regional Diets

The walrus population occupies specific parts of the continental shelf of the Bering Sea in winter and mostly moves to different parts of that and the Chukchi shelf in summer. Since the benthic faunas of those areas are not the same (Neiman 1960; Zenkevich 1963; Stoker 1978), the feeding habits of the walruses using them probably differ correspondingly. The available data on seasonal and regional feeding habits suggest such differences.

Winter: St. Lawrence concentration area.—Stomach contents have been examined from only two walruses taken in the St. Lawrence concentration area in winter (January 1957 and February 1970). Predominant in abundance and volume in these were siphons of *Mya* sp. and whole specimens of *Pelonaia corrugata.* Lesser amounts of large gastropods (feet only), feet and siphons of *Serripes groenlandicus* and *Mya truncata*, respectively, and a few small crangonid shrimps, gammarid amphipods, and holothurians also were included. On the ice beside several breathing holes used by walruses in March 1972, S. W. Stoker and I found remains of *Pagurus* sp., *Macoma* sp., and *Musculus* sp., an intact specimen of *Neptunea heros*, and fragments of unidentified gastropod egg cases. In walrus feces from several haulout areas, we identified the undigested remains of *Echiurus echiurus*, *Priapulus caudatus*, *Nucula* sp., *Mya truncata*, *Neptunea* sp., *Natica* sp., *Polinices* sp., *Chionoecetes opilio*, and *Pelonaia corrugata.*

Winter: Bristol Bay–Pribilof concentration area.—The food items predominant in numbers and volume in the stomachs of 21 specimens taken about 220 km east of the Pribilof Islands in March and April 1976 were feet of *Serripes groenlandicus* and *Clinocardium* sp. and whole brachyuran crabs of the genus *Chionoecetes.* Smaller amounts of *Neptunea* and *Buccinum* spp., *Mya truncata*, *Hyas coarctatus*, and an unidentified tunicate also were present. In walrus feces on the ice, I found abundant remains of *Neptunea*, *Buccinum*, *Polinices*, and *Chionoecetes.*

Two specimens taken just south of the mouth of Kuskokwim Bay in January 1970 contained principally feet of *Clinocardium* sp., *Neptunea* sp., and *Buccinum* sp. The only other items in these stomachs were a few tunicates, probably of the genus *Tethyum.*

Tikhomirov (1964:283) reported that the stomachs of 50 walruses taken to the south of Nunivak Island in March 1962 contained principally "shrimps, crabs (among which were a few king crabs [*Paralithodes camtschatica*]), and in lesser amounts mollusks." Further details were not given, and because this report differs so markedly from all others, I suspect that it is inaccurate.

Spring: St. Lawrence Island–Bering Strait region.—The stomach contents of 19 walruses taken by Eskimos from Gambell in the waters off the western end of St. Lawrence Island in April and May 1975 contained a predominance of siphons of *Mya truncata*, *Hiatella arctica*, and *Mya* spp. and feet of *Serripes groenlandicus.* Of secondary importance in numbers and volume were *Nephthys*, *Neptunea*, *Buccinum*, *Hyas coarctatus*, and *Thyonidium commune.*

In 14 specimens taken to the north and northeast of Savoonga in May and June 1974 and 1975, the principal food items were siphons of *Mya* and feet of *Serripes.* Secondary to these in volume were feet of *Clinocardium* sp. and whole specimens of *Thyonidium commune.* The stomach of one additional specimen from this area in May 1958 contained several whole valves, up to 2.5 cm in diameter, of *Cyclocardia* sp.

Stomachs of seven walruses taken in Norton Sound by Eskimos from Nome, during May and June 1975, contained almost exclusively the feet of *Serripes groenlandicus.* Minute quantities ($<1\%$ by volume) of *Mya* and *Tellina* and of *Neptunea, Natica,* and *Polinices* also were present.

In 77 walruses taken in the Bering Strait area by Eskimos from King and Little Diomede islands in May and June 1975, the predominant items were siphons of *Mya* spp., and *Hiatella arctica*, and feet of *Serripes groenlandicus.* Also numerous but of secondary importance in volume were *Priapulus caudatus*, *Nephthys* sp., *Lumbrinereis* sp., and *Golfingia margaritacea*, as well as *Neptunea*, *Buccinum*, *Natica* and *Polinices*, *Yoldia hyperborea*, *Tellina lutea*, and *Thyonidium commune.* The small bivalve *Hiatella arctica*, whose contracted siphon is only about 1 cm long and weighs about 1 g, was represented by extraordinary numbers of siphons in these stomachs. These were present in 55 of the 77 walruses, 22 of which contained more than 500 of these siphons; 15 stomachs contained more than 1,000. The largest number in one stomach was 6,378. One stomach contained about 10.5 kg of flesh of the bearded seal along with a few mollusks; one other contained a large volume of "sea anemones" (actiniarian coelenterates), tentatively identified as being of the genus *Metridium.*

Brooks (1954) examined an undisclosed number of stomachs from males taken in Bering Strait in June 1952 and 1953, from which he concluded that they fed there mainly on *Mya truncata* and *Clinocardium nuttallii* and to a lesser extent on *Molpadia arctica.* Females and immature animals tended more toward taking the smaller bivalves, such as *Astarte* sp. and *Macoma calcarea*, together with *Nephthys* sp. and sipunculids. These differ from the findings in 1975 by Fay et al. (1977), in terms of most of the genera and species identified. I am uncertain whether this difference reflects a change in feeding habits or simply misidentification of the specimens by specialists assisting Brooks.

Summer: Bristol Bay.—I examined the contents of digestive tracts from three males taken on Round Island in late June 1958, but found in them only fine digesta and a few setae of *Echiurus echiurus.* Such setae were abundant also in the feces from other walruses on the hauling grounds there at that time. The only other items found (by K. W. Kenyon, personal communication) in the feces were a few valves of *Cyclocardia* sp., the largest of which was 2.7 cm in diameter.

Summer: Chukchi Sea.—Stomachs from 11 males taken near Barrow in July and August 1952 and 1953 contained mainly siphons of *Mya truncata.* The holothurian *Molpadia arctica* ranked "a poor second" (Brooks 1954). Also present were a few *Priapulus*, *Sclerocrangon* sp., *Hyas coarctatus*, and *Neptunea* sp. L. M. Shults (personal communication) examined the contents of one other stomach from that area in 1976 and found mainly *Thyonidium commune*, with lesser amounts of *Priapulus caudatus*, *Neptunea*, *Buccinum*, and *Natica.*

Nikulin (1941) reported the stomach contents of an unspecified number of animals taken mainly in Bering Strait and the western Chukchi Sea in June to August 1934, 1935, and 1937. He concluded from these that mollusks were the most important prey, as indicated by the great number of genera (11) represented. Of those, apparently, *Astarte*, *Macoma*, *Serripes*, and *Mya* were most abundant. Worms, including *Priapulus*, *Echiurus*, and two kinds of polychaetes, were rated second in importance; arthropods were rated third, and "ascidians," including *Pelonaia* and *Cucumaria* (an echinoderm) were rated last, since "they were found only in insignificant quantities." Nikulin gave no indications of the sex or age of the consumers or of the specific locations in which they were taken, and he provided no data on the frequency of occurrence, weights, or volumes of the prey.

In Krylov's (1971) material from 35 walruses taken in the vicinity of Wrangell Island (presumably in July and August) in 1960 and 1963, mollusks were most frequently recorded and apparently were the most significant prey in terms of volume. However, these were mainly the smaller forms *Macoma*, *Nucula*, *Yoldia*, and *Margarites*. Of secondary importance in abundance and volume were *Priapulus*, gammarid amphipods, crabs, the bivalves *Mactra* sp. and *Thyasira flexuosa*, holothurians, and *Pelonaia*. Tomilin and Kibal'chich (1975) reported that they found the principal foods of walruses in this area in 1972 and 1973 to be *Priapulus*, *Mya*, and *Ampelisca macrocephala*.

Autumn: St. Lawrence Island. — There are no data on the feeding habits of the Pacific walrus during the southward migration in autumn. However, the St. Lawrence Islanders repeatedly told me during the 1950's that *Tethyum aurantium* (local name *oh'pah*) often made up a major part of the stomach contents during October–December, whereas it did not occur in other seasons. This suggests a seasonal change in either the feeding habits of the walruses or the availability of this and other prey.

General observations. — In all seasons and all areas, bivalve mollusks occurred most frequently in the stomach contents, but it is not clear in all instances whether they usually made up the greatest proportion by weight. Krylov (1971) reported that mollusks made up 1.59 of 2.58 kg (62%) of the stomach contents of one animal in the Wrangell Island area in summer; Fay et al. (1977) recorded that mollusks made up 665.4 of 694.6 kg (96%) of the identifiable organic matter in the stomachs of 107 animals taken in the St. Lawrence Island to Bering Strait region in spring.

In general, the analyses of stomach contents have indicated that walruses are highly selective in their feeding. Although the stomachs of animals taken in a given area tended to contain a few examples of most of the macrofaunal invertebrates known to occur there, they did not contain anything approaching a representative sample of the local fauna (Vibe 1950; Fay et al. 1977). Some organisms such as the very abundant brittle stars (Ophiuroidea) were not represented at all, whereas the larger bivalves in particular were overrepresented. Swift, elusive prey, such as fishes, shrimps, and cephalopods were scarce. Apparently, female walruses tend to select smaller prey than do males, for Fay et al. (1977) found that the unit weight of food items in stomachs of adult males was 5 to 10 times greater than in adult females.

Flesh of other pinnipeds has been found frequently enough (1 to 11%) in the stomach contents of walruses throughout the Arctic to indicate that it is an important complement to the basic molluscan fare (Johansen 1912; Gray 1927; Pedersen 1931; Chapskii 1936; Tsalkin 1937; Nikulin 1941; Vibe 1950; Brooks 1954; Mansfield 1958*a*; Loughrey 1959; Shustov 1969; Krylov 1971; Fay et al. 1977). Chapskii (1936) and Vibe (1950) presumed that walruses eat seals only when other foods are not readily available. However, the presence of seal flesh in stomachs of walruses taken in Bering Strait in spring (Brooks 1954; Fay et al. 1977; J. J. Burns and L. F. Lowry, personal communication) does not conform to that explanation, for this is an area of shallow water with an abundant molluscan fauna and little or no restrictive ice conditions. Furthermore, in three of five instances known to me, invertebrate prey were found in the stomachs with the seal flesh. Nine of 11 seal-eating walruses identified to sex have been adult males (Chapskii 1936; Mansfield 1958*a*; Rausch 1970; Fay et al. 1977; L. F. Lowry, personal communication), which suggests that this carnivory is basically a masculine habit.

Rate of Intake of Food per Day

Vibe (1950:35) reported that walruses in the Thule District of northwestern Greenland in summer tend to come inshore to feed for 4 to 6 h during each flood tide, at depths ranging from 15 to 25 m. After filling their stomachs, they withdraw "at ebb, either to continue foraging at greater depths, or to go to sleep on a drifting ice floe." This finding suggests that the animals tend to fill their stomach twice per day and to spend a total of about 8 to 12 h in doing so.

The full stomach of an adult male, according to Brooks (1954), weighed 49.4 kg. Based on the findings of Fay et al. (1977), about 5.4 kg of that would have been the weight of the stomach itself, and about 0.5 kg would have been the weight of inorganic sediments; hence the total weight of the food in the full stomach probably was about 43.5 kg. That this was an exceptionally large amount is suggested by the findings of Krylov (1971), who recorded the largest amount in any one stomach as 5 kg, and Fay et al. (1977), who found the largest amount in 107 stomachs to be 25 kg. Assuming that these maxima (43.5 and 25 kg) are representative of recently filled stomachs, and that, as Vibe (1950) has indicated, walruses tend to fill their stomach twice per day, the total daily intake of food may be between about 50 and 85 kg. That this is a reasonably close estimate of the daily rate of consumption is indicated by the feeding rates of captive walruses reported by Reventlow (1951), Bridges (1953), Hagenbeck (1963), Brown and Asper (1966), and G. C. Ray (personal communication).

Nine young walruses that were reared in captivity on diets made up mainly of oily fishes (herring, *Clupea harengus;* bonito, *Sarda chiliensis*) and clam meats (mainly *Mya arenaria*), consumed these foods in amounts ranging from 4.2 to 6.2% of their total body weight per day (Table 24). At that rate, the average free-living adult female (at TBW = 820 kg) would consume between 34 and 51 kg of food per day, and the average adult male (at TBW = 1,200 kg) between 50 and 74 kg per day. These amounts are about equivalent to filling the stomach twice per day. They may be somewhat lower than the actual rates, for the gross energy content per unit weight of the foods eaten by the captive animals was higher than that of most of the foods eaten by free-living walruses. Although the free-living walruses reside in a colder environment, they probably do not expend more energy in thermoregulation than the captives, but they do expend more in acquiring their food.

The approximate gross energy values of the daily food intakes of the captive walruses, on the basis of caloric values given by Spector (1956), were about 63 to 121 kcal/kg TBW per day. In terms of "metabolic body size" (= TBW $kg^{3/4}$),

Table 24. *Approximate gross quantities and qualities of food eaten daily by walruses reared in captivity.*

			Daily intake			Gross energy intake (kcal per day)		
Sex	Age (years)	Total body wt (kg)	kg	(% TBW)	Diet constituents[a]	Total	Per kg$^{3/4}$ of TBW	Source[b]
?	1.5	250[c]	10.5	(4.2)	10 kg herring, 0.5 L codliver oil	22,500	358	H
M	1.5	349	20.2	(5.8)	18.1 kg fish (?herring), 1.2 L evap. milk, 0.7 L veg. oil, 0.1 L codliver oil	42,142	522	Br
M	2.5	550[c]	34.0	(6.2)	50% clams (without shells), 50% herring	46,021	405	Ra
F	3	392	18.1	(4.6)	50% clams (without shells), 50% bonito	24,546	279	BA, Bw
M	3	642	27.2	(4.2)	Same	36,817	289	BA, Bw
F	4	430	22.6	(5.3)	Same	30,683	325	BA, Bw
M	4	750	36.2	(4.8)	Same	49,091	342	BA, Bw
F	4–5	400[c]	25.0	(6.2)	Herring	47,500	531	R
M	7	700[c]	38.5	(5.5)	50% clams (without shells), 50% herring	52,159	383	Ra

[a] Approximate caloric values (kcal/g): herring and mackerel (bonito) = 1.9, evaporated milk = 1.08, vegetable oil = 8.0, codliver oil = 7.0, "clams" (mainly *Mya arenaria*) = 0.8 (based on Spector, 1956).

[b] BA = Brown and Asper (1966), Br = Bridges (1953), Bw = D. H. Brown (personal communication), H = Hagenbeck (1963), R = Reventlow (1951), Ra = G. C. Ray (personal communication).

[c] Estimation, based on weight/age curve, Fig. 20.

these animals consumed about 280 to 530 kcal/kg$^{3/4}$ per day (Table 24). The mean intake in these terms, 380 kcal/kg$^{3/4}$ per day, was similar to that for maximal intakes by domestic animals reported by Kleiber (1961).

Based on these gross caloric intakes by walruses in captivity, I estimated the rates of consumption of food (kg per day) for free-living walruses of different body weights, assuming that their intake would be mainly bivalve mollusks (as indicated by Fay et al. 1977). The results (Table 25) suggest that the mean rates of consumption of benthic invertebrates by free-living walruses may be at least 5 to 7% of their TBW per day. One should bear in mind, however, that these are *net* rates of predation, for the walrus eats only the exposed soft parts of shelled mollusks, not the whole organism. Since those soft parts (foot, siphon) amount to no more than one-fourth to one-third of the total weight of the mollusks, the biomass of *gross* rate of predation will be three to four times that of the parts actually ingested. Thus, the 1,000-kg walrus that consumes 60 kg of molluscan feet and siphons per day actually will destroy about 180 to 240 kg (wet weight biomass) per day of those mollusks.

Assuming that the Pacific walrus population currently comprises about 200,000 animals and that its sex and age compositions are about as estimated for the 1972 population (see chapter on Population), then the average TBW per individual is about 720 kg, and the average *net* rate of intake of food is about 6.2% of TBW per day. For this population as a whole, about 8,900 tons of food will be consumed daily and about 3.25×10^6 tons per year. If 96% of that intake is molluscan soft parts (mainly feet and siphons) and 4% is other organisms, swallowed whole (Fay et al. 1977), then the *gross* rate of predation on benthic invertebrates may amount to a biomass of between 9.5 and 12.6×10^6 tons per year, or about 2.5 to 3% of the estimated standing stock of benthos on the Bering–Chukchi shelf. This would be a small proportion if the walrus were the only user of the benthic fauna and were nonselective in its feeding. Being a predator on certain kinds of mollusks, mainly in shallow waters, the walrus can utilize less than one-third of the total shelf biomass, and this is fed on by a wide variety of other organisms, including fishes, crabs, sea stars, cephalopods, birds, seals, and cetaceans. Furthermore, because walruses do not distribute themselves uniformly over the Bering–Chukchi shelf, the population probably has a much greater impact on the resources of some areas than of others (Fay et al. 1977). The greatest impact appears to be on the wintering areas, and I believe it is there that food may exert its greatest influence as a limiting factor on population growth.

In the wintering areas, the intake of food by the breeding adult males appears to be small, but this probably is more than compensated by the increased intake by pregnant and lactating females, whose daily rate of consumption is likely to be two to three times that of nonpregnant, nonlactating animals. During two expeditions on icebreaking ships in the St. Lawrence concentration area in late February to mid-April, I observed that nearly all of the late-term pregnant females sighted were in the water, apparently feeding, whereas more than half of the other females were sleeping or just swimming when sighted.

During the northward migration in spring (April–June), I observed that the animals taken in the harvest at St. Lawrence Island showed a reversal of that tendency for different feeding rates. Those most often having food in the stomach

Table 25. *Estimated quantities of food (invertebrates) ingested daily by individual free-living walruses, based on gross energy intake (GEI) of walruses reared in captivity.*[a]

Total body wt (kg)	Amount of food[b] eaten at gross energy intake rates					
	GEI Minimum 280 kcal/$kg^{3/4}$ per day		GEI Maximum 530 kcal/$kg^{3/4}$ per day		GEI Mean 380 kcal/$kg^{3/4}$ per day	
	kg eaten	% TBW	kg eaten	% TBW	kg eaten	% TBW
400	21.1	5.3	40.1	10.0	28.8	7.2
500	25.1	5.0	47.5	9.5	34.1	6.8
600	28.8	4.8	54.5	9.1	39.1	6.5
700	32.3	4.6	61.2	8.7	43.9	6.3
800	35.7	4.5	67.5	8.4	48.4	6.0
900	39.0	4.3	73.8	8.2	52.9	5.9
1,000	42.3	4.2	79.8	8.0	57.2	5.7
1,100	45.3	4.1	85.8	7.8	61.5	5.6
1,200	48.4	4.0	91.6	7.6	65.7	5.5
1,300	51.4	4.0	97.3	7.5	69.8	5.4
1,400	54.4	3.9	102.8	7.3	73.7	5.3

[a] Gross energy intakes are the range and mean kcal/$kg^{3/4}$ per day from Table 24.

[b] Based on 95.8% mollusks and 4.2% other invertebrates in 694.6 kg of identifiable prey in stomachs of 107 walruses from the St. Lawrence Island–Bering Strait area, and caloric values of 1,200 kcal/kg for clam meats and 850 kcal/kg for all other invertebrates consumed (Fay et al. 1977).

at that time were the adult males (25/62 = 40%); those least often containing food were the adult females with newborn calves (3/46 = 6%). All others were intermediate between those extremes (6/27 = 22%). Because a large proportion of the adult males remains in the Bering Sea throughout the summer, presumably continuing to feed intensively, the resources of the summering areas in the Chukchi Sea are available mainly to the females and young.

Feeding Behavior

Feeding Rhythm

Loughrey (1959) reported that the walruses in Hudson Bay seemed to feed mainly in the early morning hours, whereas Vibe (1950) indicated that their feeding schedule in summer in northwestern Greenland was linked more with the tides. Tomilin and Kibal'chich (1975) and Nyholm (1975) observed walruses feeding at various times during the day and night. During more than 50 whaling and walrus hunting trips with the St. Lawrence Islanders in March to June, I sighted walruses in the water more often in the morning and evening than at other times, and observed that those taken in early morning and late evening most often had food in their stomachs.

Fay and Ray (1968) recorded the diurnal activity schedule of walruses in captivity, thinking that it might resemble that of the free-living animals. Their data indicated two peaks of activity in the water, one in mid-morning to late morning, and the other in late afternoon and evening. Comparative data from sightings of walruses during shipboard and aerial surveys, however, have not confirmed that pattern (Fig. 101). Although each curve suggests that there are two or three periods per day when the animals tended to be in the water (principally feeding?), none of the curves closely resembles any of the others in regard to the timing of those periods, and none resembles the pattern shown by the captives. Thus, it seems that the Pacific walrus does not have any regular diel periodicity that could be related to feeding, possibly because the prey are relatively immobile and not rhythmic in availability.

Depth and Duration of Feeding Dives

The duration of feeding dives presumably is a function of the water depth and abundance of food, as well as the capability of the diver. The observations reported thus far seem to bear that out. Nyholm (1975) recorded the surface and subsurface times of walruses during 42 feeding dives at depths ranging from 6.4 to 12.1 m. In the shallowest water, the mean subsurface time was 2 min and the surface time about the same. In the deeper water, the animals were beneath the surface for nearly 5 min, and 2.5 min at the surface between dives. Freuchen (1935) observed two walruses feeding in water that was about 10 m deep and noted that they remained beneath the surface for 2 to 3 min per dive.

Tomilin and Kibal'chich (1975) reported that walruses feeding near Wrangell Island did so in groups of two or three animals, which dove and surfaced in unison. They watched one pair feeding in 40 m of water for about 4 h, during which the dives ranged in duration from 6 min 3 s to 9 min 7 s, and the surface intervals between dives were from 55 to 77 s. The dives of another feeding pair

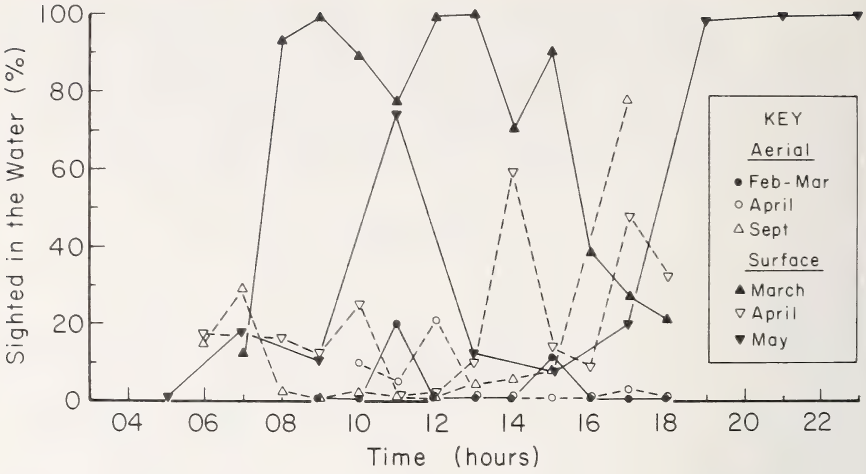


Fig. 101. Percentage frequency of occurrence per hour of walruses sighted in the water (versus on ice). Data from aerial and surface surveys of the Bering Sea (February–May) and one aerial survey of the Chukchi Sea (September). Sample sizes: aerial—February–March 14,814, April 23,550, September 11,094; surface—March 2,718, April 3,478, May 2,721. (From K. W. Kenyon, J. A. Estes, and F. H. Fay, unpublished data)

ranged from 4.5 to 5.5 min, and mean surface time was 55 s between dives.

E. H. Miller, G. C. Ray, and I observed a group of about 50 adult females and young feeding continuously for more than 5 h at a depth of 50 m. The animals surfaced and dove nearly in unison and remained beneath the surface for about 7 to 9 min per dive. One individual's surface interval between dives was 1 min 25 s. I watched another adult female feeding at a depth of 55 m, and timed two of her dives. The first was 5 min and the second 6 min 15 s; surface intervals following each dive were 45 and 60 s, respectively.

J. A. Estes and I observed a single adult male for about 2 h while it fed at a depth of 79 m. During that time, the walrus completed 12 dives, 8 of which ranged in duration from 9 min to 10 min 2 s; the other 4 dives were much shorter (2 min 10 s to 7 min 22 s). Surface times between the longer dives ranged from 1 min 18 s to 2 min 6 s; those between the shorter dives were from 31 s to 1 min 45 s. Loughrey (1959) reported feeding dives of up to 10 min duration, with about 3 min at the surface between dives; Johansen (1912) reported feeding dives of about 10 min duration in water 70 m deep.

The mean subsurface times indicated by these observations show a tendency toward positive correlation with depth, but the relation is not close (Table 26). Inexplicably, the surface intervals between dives seem to be negatively correlated with dive duration. The ratio of surface to subsurface time in the samples as a whole ranged from about 1:1 to 1:8. For those in the Bering–Chukchi region, at depths most representative of walrus habitat there, the range was about 1:5 to 1:8 (mean, about 1:6.5). This is comparable to the ratio given by Ray and Watkins (1975) for male walruses in mating displays (1:5.3) and suggests that

Table 26. *Depth and duration of feeding dives of walruses.*

Depth (m)	Number of observations	Mean duration (min/s) Surface	Mean duration (min/s) Subsurface	Surface: subsurface time ratio	Source[a]
6.4	10	2/08	2/01	1:0.9	NY
8.2	4	2/26	4/59	1:2.0	NY
9.0	20	2/28	4/46	1:1.9	NY
12.1	8	2/48	4/53	1:1.7	NY
40	?[b]	0/55	5/0	1:5.4	TK
40	20[c]	1/04	8/20	1:7.8	TK
55	2	0/52	5/38	1:6.5	U
79	12	1/34	7/46	1:5.0	FE

[a] FE = F. H. Fay and J. A. Estes (unpublished data), NY = Nyholm (1975), TK = Tomilin and Kibal'chich (1975), U = F. H. Fay (unpublished data).
[b] Number of observations not given.
[c] Approximate; exact number not given.

Pacific walruses in general tend to ventilate at the surface for about 1 min, after every 5 to 8 min of subsurface activity.

The maximum depth at which walruses can feed, according to Vibe (1950) is about 80 m. Although many have been sighted in deeper waters of the Bering and Chukchi seas, none have been identified as feeding at depths greater than 79 m.

Search for Food

Nearly all of the invertebrates that are eaten by the walrus reside on or at very shallow depths within the surface of the benthic sediments. Hence, most of them are readily accessible without extensive digging or plowing of the bottom. Because these prey are not uniformly distributed, the walrus must have the ability to locate clumps or "patches" of suitable prey and by tactual or visual means to distinguish them from other organisms and from inanimate objects.

Johansen (1912:214) claimed to have observed walruses in search of food under natural conditions, presumably having viewed them from above as they dove in clear, shallow water. Unfortunately, his description of their methods is somewhat ambiguous, for he stated that, "with regard to the manner in which the animals obtain their food, it was observed that they sink down to the bottom in a sloping direction (the front end downmost), until they almost stand on their head; they then move *backwards* ploughing the bottom with their tusks." I have added the italics since the meaning of this statement is dependent on interpretation of "backwards" in this context. One must mentally "stand on his head" to recognize that it could mean *dorsally* (literally "toward the back"), whereby the tusks would have been "ploughing the bottom" by being dragged through it, rather than thrust point-first into the sediments.

That the animals generally move snout-first along the bottom, dragging their tusks, rather than moving posteriad, digging or plowing with the tusks, is indicated by their method of propulsion with the hind limbs, patterns of abrasion on the tusks, and vibrissae, and by the search behavior of captive

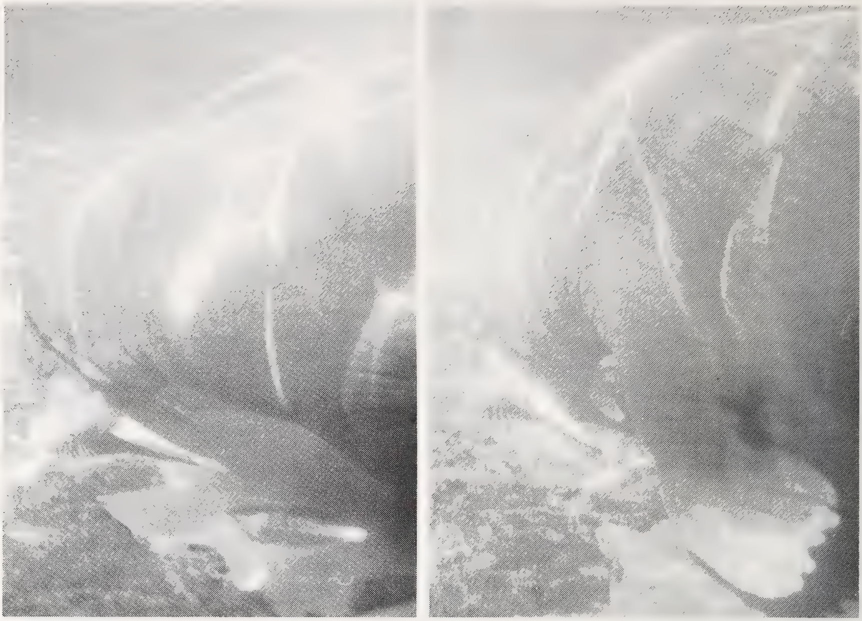


Fig. 102. Subadult male Pacific walrus in tactual exploration of the bottom of the pool at Marineland, California. While moving head-first along that surface, the animal used his forelimbs as stabilizers and hind limbs for propulsion, while maintaining constant contact of snout and vibrissae (and occasionally the tusks) with the bottom. (Photos by F. H. Fay)

walruses. The captives spend much of their time exploring the bottom of their pool in a manner that I suspect is comparable to the normal food-search pattern of free-living walruses (Fig. 102). They move forward with the body at an angle of about 10 to 45°, propelling themselves with their hind flippers, often stabilizing with their fore flippers, and maintaining contact of their vibrissae with the bottom. The mystacial vibrissae are perpetually in motion during this process; the eyes usually are closed, and the tusks simply are dragged along. The angle of intercept of the tusks with the bottom is about 20 to 30°, which is consistent with the pattern of striations made by abrasive particles on the tusks of free-living walruses.

By progressing over the bottom in this manner, the walrus has the sensory receptors (eyes, vibrissae, lips) potentially useful for detecting prey always foremost, where they can function most efficiently. Because the walrus must feed mainly in darkness, the eyes which are comparatively smaller than those of other pinnipeds may be the least important as sensors. The animals probably locate their prey by vibrissal contact. In this mode, much of the feeding of the walrus may be more akin to grazing than to plowing or raking.

Organisms that reside deep in the sediments and require excavation probably are unearthed by "rooting" with the snout. The pattern of vibrissal abrasion, the greater cornification of the upper edge of the snout (as in swine: Macarian and

Calhoun 1966), and the powerful cephalo-cervical musculature of the walrus, are unlike those of any other pinniped. Each points to frequent use of the snout as a digging organ.

Some signs of digging by walruses were found during submarine exploration of the St. Lawrence concentration area in March 1972 by Ray (1973) and S. W. Stoker (personal communication). Many broad furrows and pits, about 25 to 30 cm wide and 15 to 20 cm deep, were sighted by them in the sandy-mud bottom where several hundred walruses had been feeding not long before. Identification of those features as having been made by feeding walruses was circumstantial, since none of the animals actually was seen creating the furrows and pits. However, all other possible causes, such as ice scouring, were reliably excluded.

Some of the walrus' prey that reside deep in the sediments may be obtained without excavation. Those such as *Spisula* sp. and, especially *Mya* spp., extend their siphon several centimeters above the sediment and are slow to react to touch. In such instances, the walrus probably grasps the siphon in its mouth and simply pulls, tearing the siphon away and leaving the body of the clam still buried in place. When *Mya* is found in walrus stomachs, it ordinarily is represented by the siphon alone, occasionally with other bits of the mantle attached. Usually, *Spisula* is represented only by the foot, but other parts (siphon, gills, stomach) occasionally are present as well, suggesting that the whole clam was unearthed before the soft parts were removed.

Selection of Prey

Preliminary sorting of benthic materials and selection of prey from among them probably is done mainly with the mystacial vibrissae. Each of these stout hairs is provided at its base with a large sensory nerve ending and musculature that permits extraordinary maneuverability, as noted earlier. According to Murie (1871) the musculature of the snout and vibrissae is more highly developed in the walrus than in any other carnivore.

When captive walruses are feeding or exploring the bottom of their tank, their vibrissae appear to have nicely coordinated tactile and motor functions. They perform in much the same way as a pair of hands or two batteries of cilia, continuously examining, sorting, and selecting the materials to be ingested or rejected. The remarkable ability of captive walruses to sense and manipulate food and other materials with the vibrissae has been mentioned many times (see Howell 1930:77; Coates and Atz 1958), and I presume that free-living walruses are no less remarkable in this respect.

Ingestion of Prey

More than half of the genera of prey that are eaten by the Pacific walrus are soft-bodied or are taken when in a soft condition (e.g., molting crabs). These usually are swallowed whole, though they often show signs of having been pinched or compressed. They usually are not cut, torn, or crushed in a manner indicative of mastication by the teeth.

The genera that make up the greatest proportion by volume of the food are mollusks, which usually are not ingested whole unless they are rather small (<3 cm in diameter). Apparently, the reason for this is that the walrus is unable to pass larger, hard objects through its digestive tract. Zoo and aquarium officials have been aware of this for some time (see Pournelle 1962; Hagenbeck 1963). Several captive specimens have died in recent years as a result of intestinal obstruction by objects no larger than 3 or 4 cm in diameter (R. M. McClung and E. D. Asper, personal communication) as well as from gastric ulcers caused by retention of such objects in the stomach (G. C. Ray, personal communication). The claim by Elliott (1886:451) that many of the whole, unbroken clams in the one stomach that he examined were "large as my clinched hands" must have been an error in judgment or recollection, for the walrus' maximum gape (about 8 × 8 cm) is not large enough to allow passage of a man's fist, nor is the esophagus capable of passing such a large, hard object.

In general, only the siphon or foot of the larger clams, cockles, mussels, and whelks are ingested, as noted previously by several investigators and described in greatest detail by Vibe (1950). Notwithstanding Elliott's (1875:162) statement to the contrary, whole, crushed clams, "shell and all," do not occur in the ingesta, unless they are very small, and then infrequently. Even such small clams as *Astarte borealis* and *Hiatella arctica*, most of which in the Bering–Chukchi region are less than 3 cm in greatest diameter, ordinarily are not swallowed whole; instead, the foot or siphon usually is removed and the shell rejected. Of some 50,000 specimens of *Hiatella* that were present in the ingesta examined by Fay et al. (1977) from walruses taken in the St. Lawrence Island-to-Bering Strait area, not more than three still had most of the broken shells attached; nearly all of the rest were represented only by the siphon.

The question of how the siphons and feet are selectively removed and ingested without the shells has been the object of much speculation. Malmgren's (1864 *in* Allen 1880:136) hypothesis, that the shells are crushed with the cheek teeth, then expelled, and the soft parts swallowed, has been most widely accepted. Conversely, Freuchen (1936 *in* Mohr 1952:254–255) and Freuchen and Salomonsen (1958) hypothesized that the mollusks (along with sediments and stones) are carried upward with the forelimbs, while allowing the stones and sediments to fall away and sink to the bottom. Then, the molluscan shells are crushed between the palms, and the semi-suspended soft parts are ingested after the heavier shells settle to the bottom. This hypothesis never has been widely accepted, for as Mohr (1952:255) pointed out, some shells and especially stones are found in the ingesta frequently enough to indicate that this is not the usual method employed.

The Malmgren hypothesis also is untenable, for as I showed in the section on Dentition, the patterns of abrasion and attrition on the cheek teeth indicate that large, hard objects such as molluscan shells ordinarily are not taken into the mouth beyond the incisive area. None of the postcanine teeth shows any signs of frequent contact with such objects; only the vestigial incisors and, occasionally, the anteriormost surfaces of I^3 and C_1 are harshly abraded, presumably from frequent contact with molluscan shells. The shape and musculature of the mandible provide further evidence in support of that contention.

The walrus' mandible is different in form from that of the sea otter, *Enhydra lutris*, the only marine mammal that is definitely known to crush shells of marine invertebrates, including mollusks, with its postcanine teeth (Kenyon 1969). In the sea otter, the mandible is comparable to that of other carnivores, in that the temporal and masseter–pterygoid muscles have large, nearly equal moment arms, and the muscles themselves are large and strong, capable of accommodating a large vertical force on the principal postcanine teeth (cf. Smith and Savage 1959). The mandible of the sea otter also is structurally adapted for that kind of occlusive force, inasmuch as it shows great thickening in an inverted arc, roughly from the coronoid to P_4, the largest crushing tooth in the jaw (Fig. 103). In the walrus, the moment arm of the temporal muscle is somewhat smaller than that of other otarioid pinnipeds, and that of the masseter–pterygoid is much smaller. The temporal muscle is of moderate to large size; the masseter is very small, and the pterygoid not much larger. The mandible is greatly thickened along the anterior ramus of the coronoid, and this structural strength is carried forward in an inverted arc to the symphysis and incisive area, rather than to the canine–postcanine toothrow. The bone supporting the base of the postcanine teeth is the thinnest part of the mandible. Each mandibular ramus of the walrus is a nearly perfect example of a cantilevered parabolic girder, shaped to accommodate occlusive force principally on its anterior end (cf. Thompson, 1942:996), with compensatory force exerted mainly by the temporal muscle. The pattern of trabeculae within the mandible also seems consistent with that observation (Fig. 104). Additional upward force probably is provided by the buccinator muscle, which is unusually large in the walrus and is situated about midway along the jaw, where it has a large moment arm.

The mandibular symphysis of the sea otter is not firmly ankylosed, as it is in the walrus, but is joined by a soft fibrocartilaginous cushion which "seems to function to facilitate fitting the teeth to the object that is to be crushed" (R. P. Scapino *in* Kenyon, 1969:43). Scapino notes further that "this joint consistently shows high mobility . . . in those large carnivores that are powerful crushers." In the walrus, the symphysial joint is fused and immobile, and there is no lateral or vertical flexibility at the condyles. The mandible is capable only of vertical motion.

The incisive area is covered by an extraordinarily tough, firm gingiva, unlike that on any other part of the mouth but closely resembling the skin on the palms and soles of the flippers. This rough, cornified surface seems admirably suited for grasping and holding slippery prey; I believe that it functions also to hold molluscan shells while their contents are removed by suction.

The hypothesis that walruses use suction to remove the soft parts from the shells of mollusks was proposed first by Vibe (1950), who deduced this from comparison of the stomach contents with intact mollusks. Vibe observed that those bivalves whose shells are open at both ends, even when tightly shut, could easily be sucked out, since "there is no great vacuum to conquer." He also suggested that gastropods might be removed from their shell in the same way. From a few simple tests done with walruses in captivity, I conclude that Vibe's hypothesis is tenable. Those tests were as follows:

- In June 1958, I was present in the New York Aquarium at a regular feeding of Olaf, a 3-year-old male walrus that had been in captivity since infancy (Coats and Atz 1958). At the time of my visit, his daily ration consisted entirely of soft-shelled clams (*Mya arenaria*) that were prepared for him only by removal of the shells. I selected one of the larger of those shell-free clams; holding it firmly in my fist with only the siphon exposed, I offered it to the walrus. He took my fist in his lips and, in an instant, removed the siphon by suction and swallowed it,

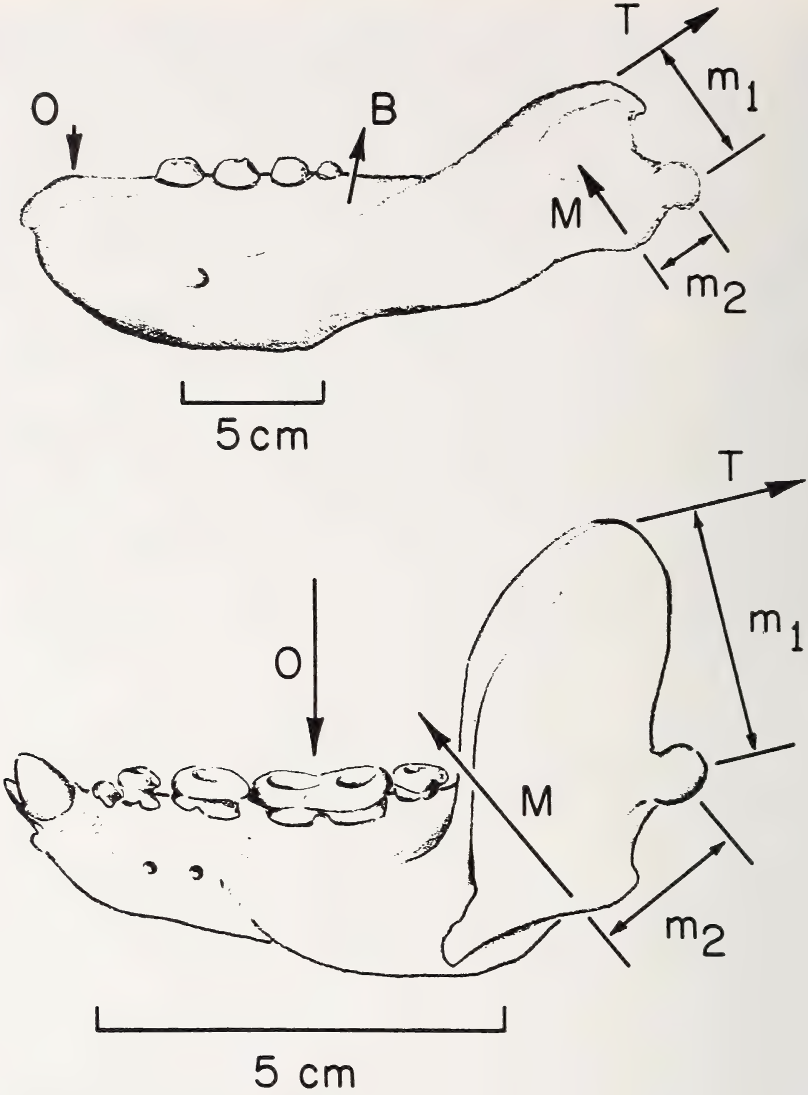


Fig. 103. Comparative mandibular mechanics in the walrus (upper) and sea otter (lower). The approximate relative strength and direction of forces applied by the temporal muscle (T) and by the masseter and pterygoid muscles (M), in relation to their moment arms (m_1, m_2), suggest that the sea otter's mandible and jaw musculature are adapted to exert a large crushing force (O) principally on the fourth postcanine, which is the largest functional tooth in the jaw. The shape of the otter's mandibular ramus also indicates maximal structural strength in the area of P_3 and P_4. Conversely, the walrus' T–M musculature appears to be incapable of applying a crushing force on the cheek teeth but capable of exerting a weak percussive force in that area. The parabolic beam of the walrus' jaw resembles those of other otarioid pinnipeds and suggests adaptation to maximal or most frequent occlusive force (O) on its anterior end. Although the T–M musculature can exert only a weak percussive force in that area, some additional pressure probably can be exerted by the unusually powerful buccinator muscle (B).

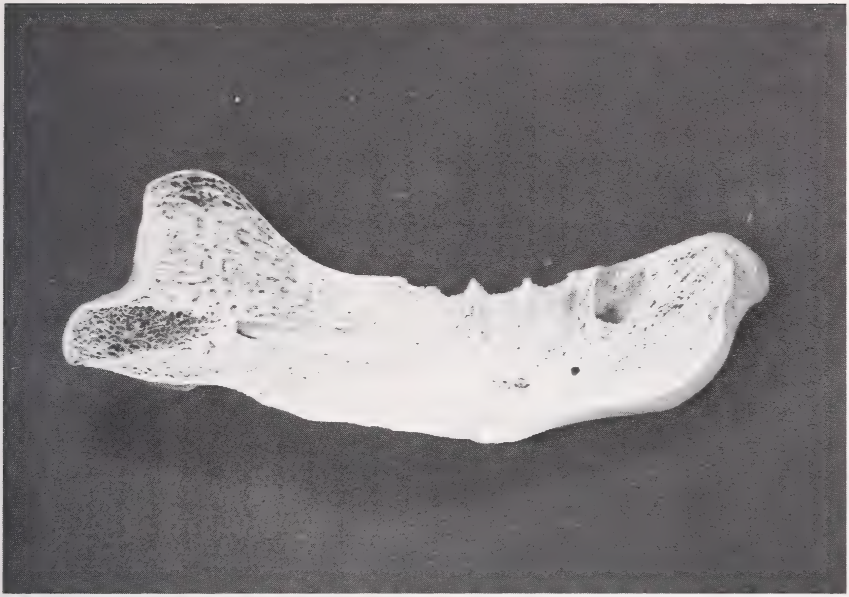


Fig. 104. Longitudinal section of the mandible of a 5-year-old female, showing orientation of trabeculae. (Photo by F. H. Fay)

leaving the remainder of the clam still in my hand. I repeated this with the same result. Thus, it was clear that the siphons of large clams could be removed by suction alone, even by a walrus with no previous experience in benthic feeding.

- In the second test, performed about 1 year later by G. C. Ray (personal communication), Olaf was given several intact specimens of *M. arenaria*, but these were not held firmly in hand. The walrus took each clam in his lips, promptly removed the siphons by suction, and ejected the broken shells (Fig. 105). The shells seemed to have been broken during manipulation of the clams with the snout and lips. Again, the animal demonstrated very clearly that the siphons could be removed by suction alone and, further, that the whole clams were not taken into the mouth beyond the incisive area.
- The third test was conducted by E. D. Asper and me at Marineland of the Pacific in 1970, using an adult female Pacific walrus and her mate. Both animals were about 9 years old and had been in captivity since infancy. Much of their normal diet was made up of small, whole herring and bonito, which they ingested by sucking them in, one by one. We attached a stiff, plastic tube to a vacuum gauge capable of registering one negative atmosphere (–30 in. of mercury) and inserted it into one of the herring, which the female took readily into her mouth. The gauge read –10 in. Hg. Repeating this process several times with each of the animals, we obtained readings on the gauge of up to –15 in. Hg (0.5 negative atmosphere) but observed that the animals also were sucking in a great amount of air around the tube. It was clear that the vacuum was stronger than our measurements had indicated. Asper continued the trials intermittently during the following year and reported (personal communication) that he had

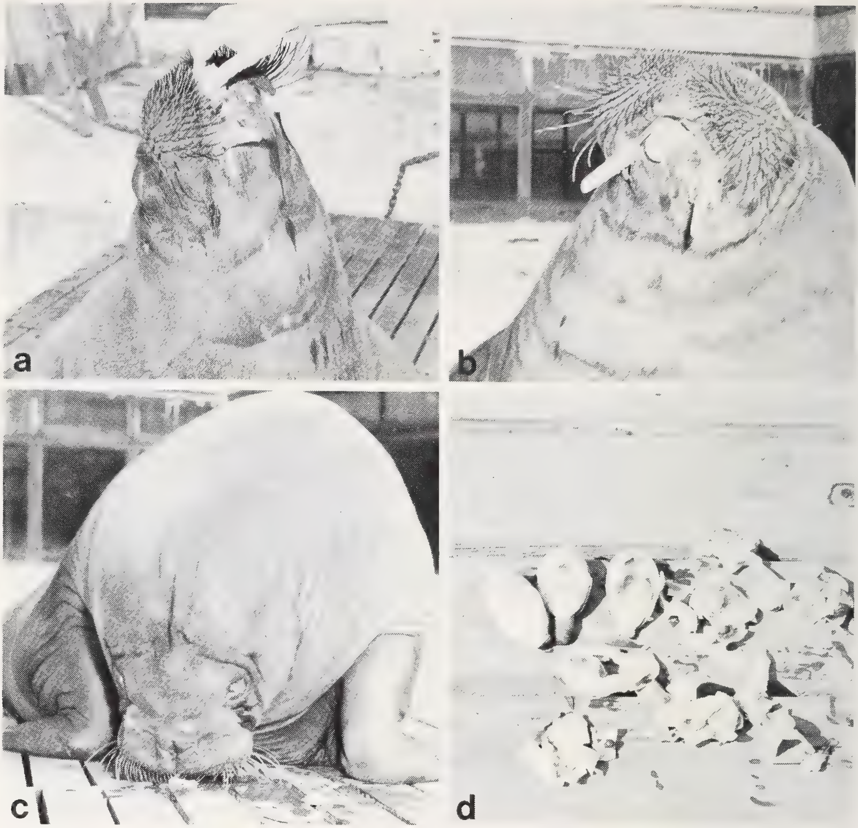


Fig. 105. Captive walrus in the New York Aquarium feeding on whole, soft-shelled clams, *Mya arenaria*: (a) the clam is taken in the lips, (b) the shells are ejected after removal of the siphon by suction, (c) the ejected shells are re-inspected tactually by means of the vibrissae; (d) view of the remains, with two intact clams (upper left) for comparison. (Photos by S. Dunton, N.Y. Zoological Society)

obtained repeated readings of "–27 in. Hg" which he felt were conservative, inasmuch as the animal was "still pulling a lot of air around the mouthpiece."

That walruses of all ages in captivity suck up their food and any other small objects in their pen, is well known to their keepers (see Reventlow 1951). Such animals in captivity also have a reputation for using their remarkable vacuum for removing paint and other coating from the walls of their tanks (G. C. Ray and D. H. Brown, personal communication) and for toying with large, noningestible objects. Hagenbeck (1963:25), in speaking of those under his care, noted that "the outlet of their swimming pool (1.10 m deep) is closed with a metal plug, weighing 5 lbs., and the walruses have no difficulty in sucking this out when the basin is full of water." He, as well as Coats and Atz (1958) and Ruempler (1976) also reported that their walruses, when given whole, large herring, very neatly sucked off all of the flesh, leaving only the skeletons.

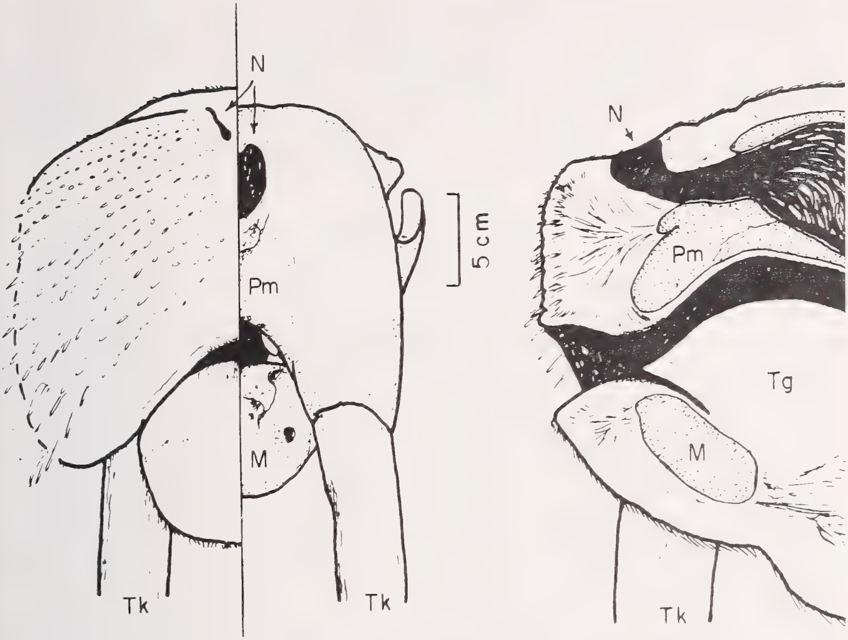


Fig. 106. General structure of the mouth of the Pacific walrus: left, anterior view with teeth fully occluded and lips slightly open; all flesh has been removed from the left side of the skull and mandible; right, same head in medial sagittal section, with mouth slightly open. N, external nares; Pm, premaxillary bone; Tg, tongue; M, mandible; and Tk, tusk. The incisive surfaces of the mandible and premaxilla do not meet when the mouth is closed to its maximum; only the ample lips can seal the oral entrance. (Adapted from photos by F. H. Fay)

The extraordinary "vacuum pump" of the walrus, by means of which this suction is accomplished, is powered by very large lingual retractors and depressors (*m. styloglossus*, *hyoglossus*, and *genioglossus*), complemented by the highly vaulted palate, the long, firmly ankylosed mandibular symphysis, and the unusually powerful *m. tensor veli palatini* and *m. buccinatorius*, which provide rigidity to the walls of the "cylinder." The tongue is the "piston." The small, rigid oral aperture, complemented by ample, muscular lips, insure that the full effect of the vacuum is exerted only on objects held in the incisive area at the front of the mouth (Fig. 106).

In his exploration of the sea floor in an area where walruses had been feeding, S. W. Stoker (personal communication) observed that visibility was obscured not only by low light intensity but by high turbidity near the bottom. Stoker and I speculated that the turbidity was due to the activity of the walruses, stirring up the sediments in the course of their search for food. The importance of tactile organs for locating and identifying prey in such a dark, murky habitat was incontrovertable. Also, the need for a swift, efficient method to remove 40 kg per day of siphons and feet from the small mollusks that resided there was abundantly evident. Although many of the details of the actual search and ingestion process will remain obscure until the animals can be closely observed under natural conditions, the important factors now appear to be the strong, sensitive snout and oral suction, rather than the eyes, tusks, and crushing teeth. The tusks appear to function mainly as social display organs and weapons; the function of the cheek teeth, if not in alimentation, remains unclear.

Reproduction

Reviewing the earlier recorded knowledge of reproduction in walruses, Allen (1880) recognized that the female breeds at intervals of 2 to 3 years, gestation lasts about 1 year, and a single calf is born in the spring and suckled for 1 to 2 years. Much additional information on this subject was contributed in the first half of the 20th century by Chapskii (1936), Belopol'skii (1939), and Freiman (1941), and in the second half by Brooks (1954), Mansfield (1958*a*), Popov (1960*a*), Burns (1965), Krylov (1962, 1966*b*, 1966*c*, 1967, 1969), and Gol'tsev (1975, 1978). These later studies were contemporary with mine and were developed along similar lines. My principal objectives were to describe the annual cycle of reproductive events and to relate age and physical development to reproductive performance.

I examined both males and females. For the males each testis was weighed to the nearest gram, with and without epididymis, and measured in length and width to the nearest millimeter. Immediately thereafter, a 2 × 10 × 10 mm sample from the body of each testis and a similar slice from the mid-body of the epididymis were fixed in AFA or 10% formalin. These tissues were dehydrated in ethanol, embedded in paraffin, serially sectioned at 7–10 μm, stained in hematoxylin–eosin, and mounted on glass slides in Permount for microscopic examination. For each specimen, the seminiferous tubules and epididymal ducts were measured in 10 cross-sectional diameters taken at random. Histological conditions in the tubules and ducts were interpreted principally on the basis of Leblond and Clermont (1952), Ortavant (1959), and Roosen-Runge (1962).

The uterus of each female was examined in the field within a few hours after acquisition, at which time the ovaries were excised and fixed whole in 10% formalin for later examination in the laboratory. The length and diameter of each horn were measured, and the uterus was split open entirely and searched for embryos and for endometrial lesions (placental scars) at the site of previous placental attachment. The width, position, and color of each placental scar were recorded, and the age of the scar from parturition to collection of the specimen was estimated on the basis that: (1) the placental scar in animals known to have given birth less than 24 h earlier was about 15 to 25 cm wide and was very rough and bloody; (2) in females with calves estimated to have been 3 to 4 weeks old (based on comparison with calves held in captivity), the healed scar was about 4 cm wide and deep reddish brown; (3) in females 6 months postpartum, the placental scar was dark brown and about 3.5 cm wide; (4) 1 year after parturition, the scar was orange-brown and 3 to 3.5 cm wide; (5) after 2 years, the scar was yellow-orange and about 2.5 cm wide; and (6) after 3 years it was pale yellow and about 2 cm wide. Occasionally, I found an indistinct yellowish scar, 1 to 1.5 cm wide, that I judged to have been at least 4 years old.

The preserved ovaries were serially sectioned in 2- to 3-mm-thick slices and were examined visually, without magnification. For interpretation of their structural features, I referred mainly to Maximov and Bloom (1948), Ham (1950), Cole and Cupps (1959), Enders (1963), Craig (1964), and Harrison and Weir (1977).

Definitions

As the terminology that I use in the following account was drawn from several sources and may not be universally understood, some definitions and indications of the limits of my interpretations are necessary.

Spermatogenesis is the entire process of development of the primary male germ cells, beginning with the "dormant" spermatogonia and ending with the release of free spermatozoa into the lumina of the seminiferous tubules. In the following description of testis development, I have used this term also as the name for the entire period in which the process takes place. That period is divisible into two parts, recrudescence and spermiogenesis.

Recrudescence is the prolonged, initial part of spermatogenesis, when the spermatogonia undergo premeiotic divisions and eventually are transformed, meiotically, into spermatocytes. It ends with the maturation division of secondary spermatocytes to form spermatids.

Spermiogenesis is the final part of spermatogenesis, beginning with the first appearance of spermatids and ending with the last release of spermatozoa; it is followed by retrogression of the seminiferous epithelium.

Retrogression begins when the ranks of secondary germ cells degenerate and pass into the lumina of the tubules. At its conclusion, only the spermatogonia and Sertoli cells remain. This is a period of quiescence, followed by recrudescence.

In the description of developments in the seminiferous epithelium, I have reported only the two general types of *spermatogonia*: type A with a nucleus containing diffuse, small, chromatin granules and a prominent, round nucleolus; and type B with a large round to oval, darkly stained nucleus. Where *spermatocytes* were present, both primary and secondary types were recognized. *Spermatids* were so called from their first appearance at the end of the maturation division of secondary spermatocytes until the time of their reduction in size to spindle-shaped, deeply staining *spermatozoa*.

For describing sexual development in relation to age, males were regarded as *potent* when their testes contained spermatozoa or maturing spermatids (i.e., when they seemed potentially capable of producing mature gametes). *Fertile* males were those that had spermatozoa in the body of the epididymis, as well, and probably had attained the capacity to fertilize ova. In the male, *puberty* is the earliest appearance of potency; *adolescence* is the period from puberty to the onset of fertility. The *subadult* male is fertile, but his overall physical development is not yet complete; the *adult* male has attained full physical and reproductive maturity.

In the female, *pregnancy* is the period beginning with fertilization of the ovum and ending with birth of the calf. *Gestation* is the latter part of that period, from *implantation* (nidation) of the blastocyst until birth.

In the ovaries, all of the *follicles* that I detected visually were in their "second phase" of development; each had a fluid-filled antrum 0.5 mm in diameter or larger (Harrison and Weir 1977). Follicles in the "first phase," before development of the antrum, were seen only in histological preparations. Since follicles with antra up to 5 mm in diameter occurred commonly in the ovaries of immature females and of anestrus and pregnant adults, in any season, I assumed that this was a *resting* stage, not related to proestrus. When the antrum had increased in size to more than 10 mm in diameter, I regarded the follicle as *ripe* or in the process of rapid development from the resting stage to the level required for ovulation.

Degenerate follicles were those containing milky, caseous, or calcified material and not associated with an ovulation scar in the adjacent tunic.

The *corpus luteum of pregnancy* in the first trimester was recognized by its moderate size, about the same as that of a ripe follicle. It was pinkish to yellowish and had a distinct ovulation scar in the adjacent tunic. In longitudinal section, its outline was circular to slightly elliptical, with an irregular border among the thecal folds. In the second to fourth trimesters, it was similar in appearance to the foregoing but about twice as large, more elliptical, having a smoother perimeter, and being highly vascularized. In the fifth trimester, at or near full-term, it was slightly smaller than at the fourth trimester, pale reddish to orange-brown, and contained up to 50% fibrous tissue, usually radiating from a firm central core.

The *corpus luteum of pseudopregnancy*, resulting from release of an ovum that apparently was not fertilized, resembled the corpus luteum of pregnancy, except that it was no more than half as large and showed retrogressive signs that were greatly out of phase with the corpora in the ovaries of pregnant females. Corpora that were not associated with an adjacent ovulation scar, probably having retained the ovum, were of two types: *accessory corpora lutea* which occurred in synchrony with a corpus luteum of pregnancy, and *corpora atretica* which occurred in the absence of or not in developmental synchrony with a corpus luteum of pregnancy.

Each type of corpus luteum eventually degenerates, shrinking to a firm, fibrous scar, the *corpus albicans*. The scar of the corpus luteum of pregnancy is retained for several years, although it continues to diminish in size.

I considered any female whose ovaries contained at least one ripe follicle, corpus luteum, or corpus albicans to be *fertile*, i.e., potentially able to ovulate or having already ovulated at least once. A female that had completed at least one pregnancy was considered to be *fecund*. Any young animal that was not fertile but had 10 or more vesicular follicles 2 to 6 mm in diameter in each ovary was considered as having reached *puberty*; young fertile females that had not yet completed a pregnancy and were physically immature were considered to be *adolescent*. Physically and reproductively mature fecund females were regarded as *adults*.

Reproductive Organs

Male

The gross anatomy of the reproductive organs in a very young male walrus was described by Murie (1871). The testes of adults are more oblong than those depicted in Murie's plate, their length being 3 to 4 times the diameter (Fig. 107). They are situated outside the muscular abdominal wall, in the blubber lateral to the base of the penis, more as in the Phocidae than in the Otariidae. In the lean adult male during the mating season, however, the prominence of the greatly enlarged testes suggests some tendency toward scrotal arrangement (Fig. 108), as in the Otariidae (Scheffer 1958).

The penis lies in an abdominal sheath, and in the adult more than half of its bulk is made up of bone, the os penis or baculum. A prominent median raphé of pale, hairless skin extends from the penile orifice to the vicinity of the anus (Fig. 109). The orifice is about four-fifths the distance from anus to umbilicus. The relative growth of the baculum and of the non-spermiogenetic testes was described earlier (see Figs. 22 to 25).

Female

The anatomy of the reproductive tract of the female walrus has been described by Cleland (1900) and Burne (1909) from dissection of two pre-adolescent animals. As the tract of the adult differs somewhat from those described, a few supplementary remarks are included here.

The reproductive tract lies in the posterior third of the abdomen, ventral to the colon and dorsal to the urinary bladder. In multiparous females, the anus and entrance to the urogenital vestibule are surrounded by an area with slightly longer hair than on the rest of the body. In the preputial depression, just outside the ventral edge of the vestibular orifice, is the short, robust clitoris, the dorsal frenular fold of which is continuous with two transverse folds that presumably are homologous with the labia minora (Fig. 110). The urogenital vestibule is 15 to 20 cm long and about 6 cm in inside diameter. Near its anterior end it receives the urethra, which enters the ventral wall through a prominent papilla, 2 to 3 cm in diameter (Fig. 111). Confluent with the papilla is the hymenial fold, which separates the vestibule from the vagina. The height of this fold is about 1 cm. The vagina is 20 to 25 cm long and has about the same inside diameter as the vestibule; the walls of both are about 2 cm thick. In its anterior half, the vagina is partly divided by a median dorsal fold, which is continuous posteriad with the most prominent lobe of the hymen and, anteriad, with the oral prominence of the uterus. The oral prominence extends 3 to 5 cm into the anterior end of the vagina, with consequent deep fornices laterally and ventrally. In its posterolateral surfaces lie the separate orifices of the didelphic uterus. Anterior to this, the cervices and corpora uteri are 10 to 15 cm long, and the uterine horns, about 25 cm long and 4 cm in diameter, arc ventrolaterad to the ovaries. The relative growth of the uterine horns and os clitoridis was described earlier (see Figs. 27, 28).

The partly septate vagina and wholly didelphic uterus, with no interluminal connections between uterine cornua in the cervix or otherwise, are unique among pinnipeds and may be atavistic, rather than adaptive to conditions in an otherwise rather specialized mammal. In other otarioid seals, the lumina of the uterine horns are interconnected in the corpus and cervix uteri and have a common os externum; the phocoid seals have a common cervical canal, also with a single os externum (Cleland 1900; Sleptsov 1943; Harrison et al. 1952).

Adjacent to the end of each uterine horn and attached to it by a stout ligament

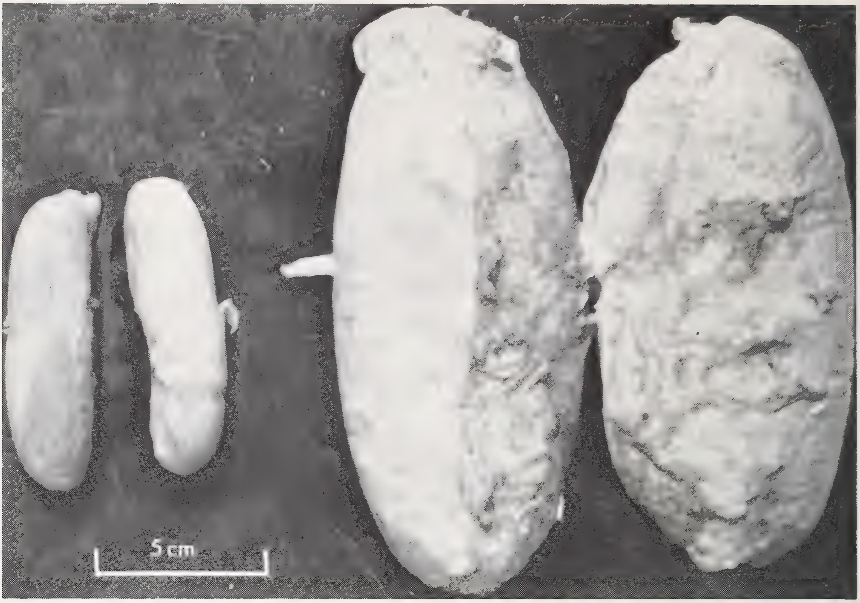


Fig. 107. Comparative shape and size of the testes of adult (right) and 1-year-old (left) Pacific walruses. (Photo by F. H. Fay)

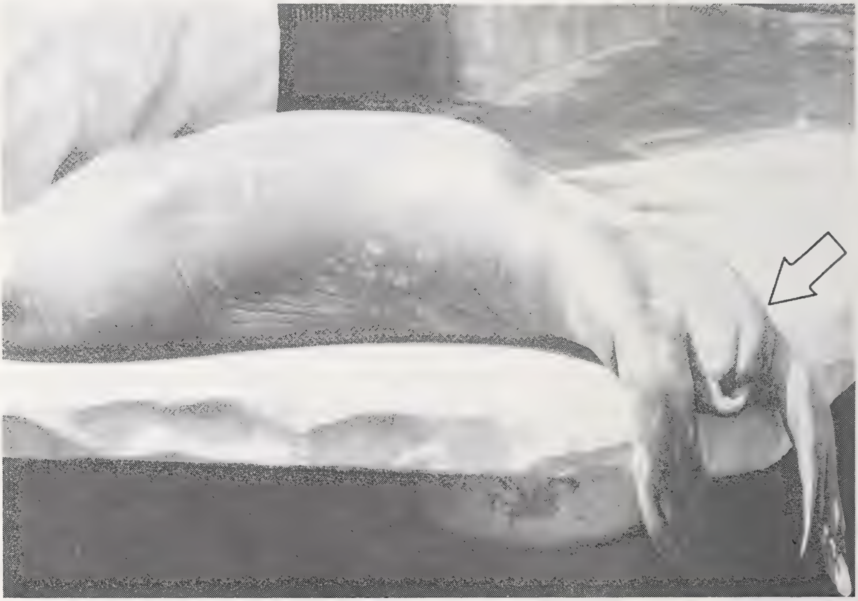


Fig. 108. Tendency toward scrotal arrangement of the testes (arrow). Posteroventral view of the hindquarters of an adult male that was reared in captivity at Marineland, California. This photo was taken in March, when the animal was exceptionally lean and the testes enlarged. (Photo by G. C. Ray)

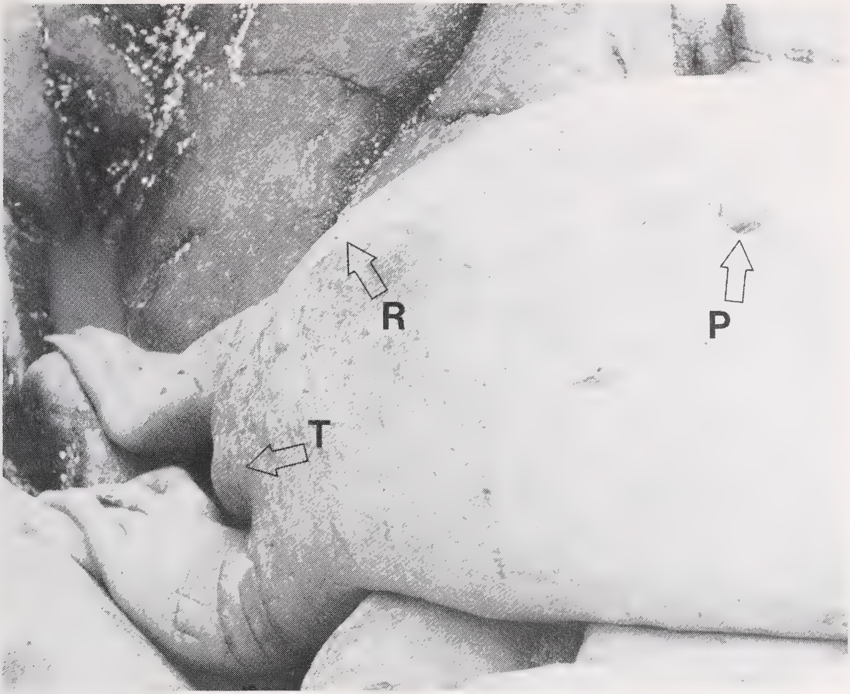


Fig. 109. Oblique ventrolateral view of the hindquarters of an adult male Pacific walrus in June at Round Island: P, penile aperture; R, midventral raphé; T, bilateral bulge of the semi-scrotal testes. (Photo by K. W. Kenyon)

is the ovary. Each ovary is enclosed in a relatively tight-fitting bursa with a small (about 2 × 1 cm) oval aperture, the bursal slit, near its uterine end. The funnel of the oviduct, with longitudinal ranks of fimbriae, surrounds all but the most anterior edge of the bursal slit and is much smaller and less elaborate than those of either phocids or otariids. From the funnel, the oviduct passes in a sinuous course around the posterior curvature of the bursa, then along its lateral surface to the ovarian ligament, which it penetrates to enter the short fallopian tube and the uterus through a minute papilla. In at least 10 females whose ovarian bursae I examined in detail, this was consistently the course of the oviduct; that is, it was not "short and straight," as described by Burne (1909:737).

In the ligaments about the ovarian bursa, I frequently found one to three fluid-filled cysts up to 2 cm in diameter. Cysts of this kind also occur frequently in other pinnipeds and occasionally in man and other mammals, where they have been identified as enlargements of rudimentary mesonephric and paramesonephric ducts (Gardner et al. 1948). Their occurrence in the walruses seemed unrelated to reproductive status, except that I found none in sexually immature animals. The cause and function of these cysts are unknown (H. W. Mossman, personal communication).

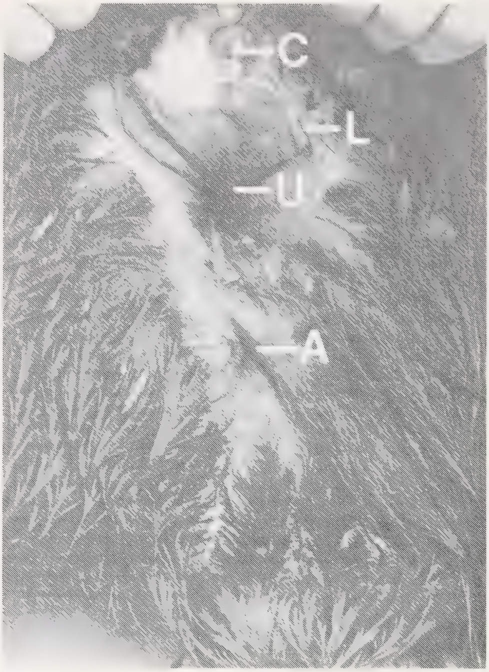
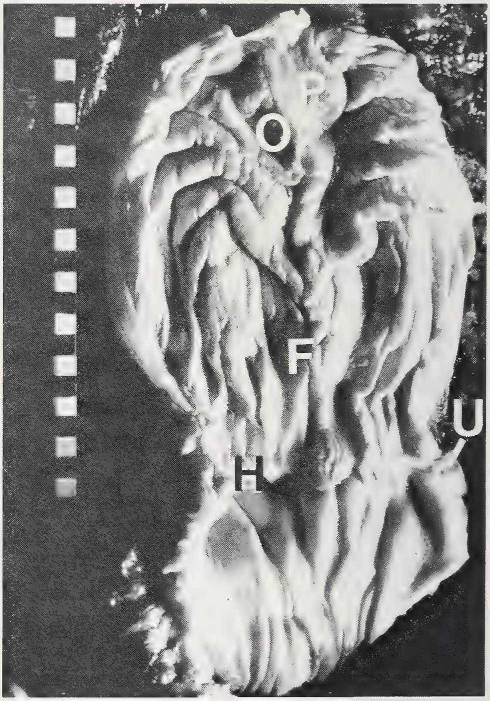


Fig. 110. Posteroventral view of the anal-urogenital area of a 3-year-old female Pacific walrus; C, clitoris; P, preputial depression; L, labia minora; U, urogenital orifice; and A, anus. The ventral side of the short tail is at lower right. (Photo by G. C. Ray)

Fig. 111. Interior of the urogenital vestibule and vagina of an adult Pacific walrus. The ventral wall has been cut longitudinally and laid open: P, oral prominence of the uterus; O, right os externum; F, median vaginal fold; H, hymenial fold; and U, urinary papilla. Scale in centimeters. (Photo by F. H. Fay)



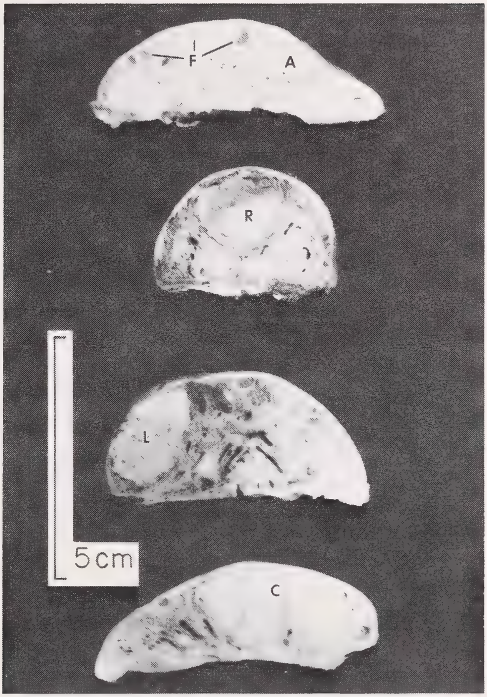


Fig. 112. Longitudinally sectioned ovaries from Pacific walruses; F, resting follicles; R, ripening follicle; L, corpus luteum derived from a single follicle; C, compound corpus luteum derived from two follicles; and A, corpus albicans. (Photo by F. H. Fay)

The ovaries of adult females are 5 to 8 cm long and 2 to 4 cm in diameter, being essentially oval and smooth. Usually, a few translucent follicles are visible beneath the tunic or bulging slightly above its regular surface (Fig. 112). In longitudinal section, those follicles appear as fluid-filled vesicles, irregularly distributed in the cortical layer, just beneath the tunic. They may occur singly or in clumps of two to six, usually with one follicle in each clump larger than the others. Ripe follicles usually are single.

The corpus luteum of pregnancy during gestation generally makes up one-third to one-half of the ovary, causing a substantial bulge. The corpus usually is derived from a single follicle, but I recorded 17 of 123 (13.8%) that were compound. Each of the compound corpora was made up of one central corpus of pregnancy with one to three adjacent accessory corpora lutea. In each instance, there was but one ovulation scar in the tunic over the central corpus. Separate accessory corpora lutea in the same or the opposite ovary were identified in three other instances (2.4%) in this series of 123 specimens.

Age at Sexual Maturity

Males

In the testes of 10 newborn males, the seminiferous tubules were small (57–68 μm in diameter) and were lined with Sertoli cells and type A spermatogonia; most of the tubules had no apparent lumen. A few cells with darkly stained nuclei, resembling those of intermediate or type B spermatogonia, seemed to be degenerating and advancing toward the center of the tubules. Similar conditions were seen also in the testes of a 1-year-old male collected in the first days of June. The tubules in the latter were smaller (39–57 μm) than those of the newborn males.

The germ cells in the testes of 2-year-old animals (two specimens) were similar to those of the newborns, but the seminiferous tubules were somewhat larger (49–81 μm), still without a lumen. The same was true of one 3-year-old, which had, however, both type A and type B spermatogonia centrally. The diameter of the seminiferous tubules in this animal ranged from 70 to 81 μm. Three animals taken in November and December of their fourth year had testes in which type A spermatogonia predominated, and there was much cellular debris centrally. Tubule diameters in these ranged from 36 to 73 μm. Two others in December of their fifth and sixth years were the same, with tubule diameters of 48 to 69 μm.

Two 5-year-olds and two 6-year-olds taken in May and early June were somewhat more advanced in testicular development, having mainly type B spermatogonia and a few primary and secondary spermatocytes. However, three of them still lacked any appreciable central lumen in the tubules, which were 90 to 107 μm in diameter. Another 6-year-old taken in July was in the same condition. The seminiferous tubules of five males taken between late November and the end of February of their seventh year, were small (54–97 μm) and, with one exception, were comparable to the 5- and 6-year-olds in regard to cellular components. The exceptional one (6.6 years on 6 December) had a few spermatids as well, some of which seemed to be mature. Two other animals taken in late March of their seventh year had much larger tubules (117–167 μm) with a small lumen, but neither contained any spermatozoa. In one of the March specimens, only Sertoli cells and spermatogonia were present; in the other were signs of retrogression, with spermatid giant cells and much other debris in the lumen. A 7-year-old specimen taken on 2 June also showed tubules in retrogressive condition.

The youngest animal in my series that had seminiferous tubules containing clusters of apparently mature spermatids and free spermatozoa in the lumen was an 8-year-old taken on 26 April. The tubules in this animal were about 150 μm in diameter. Another 8-year-old, taken on 25 May, was retrogressive, with giant cells and cellular debris in the lumina. None of four ninth year males taken in November–December was potent, but one 9-year-old taken on 25 May appeared to be retrogressive, possibly having achieved potency some time earlier. One of three animals, taken in November to March of their 10th year was potent, as were four 10-year-olds taken in April–May. One taken in August at 10.2 years and four in November–December at 10.5 to 10.6 years were not potent. One at 10.8 years taken on 19 February was potent and fertile; it had spermatozoa in the body of the epididymis as well as in the testes. The apparent nonpotency of many of the young males that were taken from July to December is not necessarily diagnostic of reproductive incapability, for most subadults seem not to come into breeding condition until mid-winter to late winter.

The implication from this small series is that some males may attain potency as early as their seventh winter or spring, but most probably attain that state no earlier than the eighth or ninth winter. These findings are similar to those of

Krylov (1967), who observed that the seminiferous tubules in most 7-year-olds taken in spring had an open lumen, and in one of four, sperm were present. He found spermatozoa in four of six 8-year-olds, in 11 of 13 9-year-olds, as well as in all older animals up to 22 years, taken in spring.

Primarily on the basis of body and tusk size, earlier Soviet investigators estimated that male walruses reach "sexual maturity" at 5 or 6 years (Chapskii 1936; Belopol'skii 1939; Freiman 1941). With fewer specimens but more accurate methods, Brooks (1954), Mansfield (1958*a*), and Krylov (1967) judged that males are not potent at 5 years but become potent a year or two later. My specimens suggest that incomplete spermiogenesis may begin as early as the fifth and sixth years, but complete spermiogenetic cycles ending in production of spermatozoa seem not to occur generally until the animals are at least 7 or 8 years old. Probably all males are potent by the time they are 10 years old.

Although the ability to produce spermatozoa is suggestive of potential ability to fertilize ova, the better test of fertility is the presence or absence of sperm in the epididymis. Since spermatozoa occur less often in the corpus epididymis than in the caput or cauda (Ortavant 1959), their presence in the mid-body of the epididymis should be a sensitive index of their abundance, hence probably also of fertility. In my sample, none of the potent animals up to 10 years old had any spermatozoa in the corpus epididymis; the youngest animal in which they were present was 10.8 years. Spermatozoa were present in nearly all of the older, potent specimens taken in winter. Krylov (1967) found some sperm in the epididymis of one 7-year-old and in most of the 8-, 9-, and 10-year-olds, as well. Regrettably, he did not indicate in which part of the epididymis he found them or exactly how he did so.

The findings that male Pacific walruses begin to produce spermatozoa when they are 7 or 8 years old but do not become capable of fertilizing females until they are about 10 years old is in agreement with the reproductive performance of Pacific walruses in captivity. A male reared at Marineland of the Pacific first showed "definite enlargement" of the testes in March and April of its eighth year (J. D. Prescott, personal communication); two others, reared in the same facility with females of the same age, sired their first calves in their 10th year (E. D. Asper, personal communication). In free-living walruses, there is secondary acceleration of growth of the testes, baculum, and body size beginning about the 8th to 10th year, as well as a change in the rate of tusk growth and in the development of the thick "bosses" in the skin of the neck and shoulders. Full sexual maturity of the free-living males is probably not attained until they are about 15 years old, when they have essentially completed the secondary growth of body, baculum, and testes, and they are sufficiently large and powerful to compete successfully with the other adult bulls for mates.

Females

Krylov (1966*b*) reported that eight females up to 4 years old, taken in July to September, had no macroscopic follicles in their ovaries, and that the horns of their uteri were slender and smooth, indicating that they had not been pregnant. I examined 10 specimens 1 to 4 years old, taken in May and June, and found that their uteri also were slender and smooth (1 to 1.5 cm in diameter), but that each had a few vesicular follicles 1 to 6 mm in diameter in both ovaries. Four others

Table 27. *Age at first ovulation and age-specific fertility rate of the Pacific walrus.*[a]

	Age class (years)								
	4	5	6	7	8	9	10	11	Total
No. ovulating first time	22	68	49	43	14	8	1	0	205
Percent ovulating first time	10.7	33.2	23.9	21.0	6.8	3.9	0.5	0	100
Age-specific fertility rate (%)	10.7	43.9	67.8	88.8	95.6	99.5	100	100	

[a]From J. J. Burns and F. H. Fay (unpublished data). No ovulation observed at age 3.

up to 4 years old examined by J. J. Burns (personal communication) in May and June had numerous small vesicular follicles; one 4-year-old specimen had one ripening follicle 13 mm in diameter. Gol'tsev (1975) found that one of six 4-year-olds taken in the Chukchi Sea in July to September was pregnant for the first time. The oldest animal in its first pregnancy reported by Gol'tsev (1975) was 9 years old; the oldest at first ovulation reported by Krylov (1966*b*) was 12 years old.

The distribution of ages at first ovulation in 205 specimens examined by J. J. Burns (unpublished data) and me (Table 27) indicates that at least 10% of the females ovulate for the first time at 4 years of age; about 68% have ovulated at least once by the time they are 6 years old, and 100% are fertile by the age of 10 years.

It should be understood that the data in Table 27 relate only to the ability to ovulate. Ovulation does not necessarily mean that the animal also has the ability to produce offspring, for first ovulations frequently do not result in successful fertilization, implantation, gestation, or birth. Sexual maturation in female walruses is a prolonged process. The animals are not sexually mature in the most conservative sense until they have attained full physical development in their 9th to 10th year, at which time they also attain the peak of their reproductive performance, as will be described further in the following parts of this report.

Annual Reproductive Cycle

Testis Cycle

An annual cycle of changing size of the testes probably begins in the Pacific walrus in the fifth or sixth year after birth and intensifies thereafter until adulthood (Table 28). Its course, in terms of histological events in the seminiferous epithelium and in the ducts of the corpus epididymis, was studied in 117 specimens more than 4 years old. For the purpose of assigning a rank to each of these, the principal cellular associations seen in the seminiferous tubules were divided into eight general types. In sequence, beginning with the onset of recrudescence and ending with retrogression, they were as follows (see Fig. 113):

Table 28. *Weight of the testis and epididymis in relation to age of non-spermiogenetic ("inactive") and spermiogenetic ("active") Pacific walruses.*

Age (years)	Testis weight (g)[a]						Epididymis weight (g)[a]					
	Inactive			Active			Inactive			Active		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
0	64	13–26	18	—	—	—	—	—	—	—	—	—
1	2	20–29	24	—	—	—	—	—	—	—	—	—
2	3	39–58	48	—	—	—	1	13	—	—	—	—
3	5	35–62	51	—	—	—	3	19–40	29	—	—	—
4	2	44–74	59	—	—	—	1	34	—	—	—	—
5	3	59–98	74	—	—	—	1	22	—	—	—	—
6	7	48–148	98	1	75	—	6	17–54	37	1	34	—
7	1	179	—	1	115	—	1	51	—	—	—	—
8	5	98–158	129	1	224	—	4	39–44	40	—	—	—
9	3	151–176	165	1	196	—	2	51–65	58	1	43	—
10	5	100–308	167	5	248–416	303	5	33–70	51	3	53–69	61
11	3	255–328	297	1	419	—	3	59–105	80	1	76	—
12	4	158–287	218	7	277–819	443	3	42–81	60	6	82–161	113
13	3	189–513	385	2	325–374	350	2	41–106	74	1	83	—
14–15	8	199–425	326	13	318–636	458	7	71–107	89	10	75–142	111
16–20	11	152–594	363	8	307–693	516	10	35–172	99	8	63–215	135
21–37	9	306–510	403	3	251–568	399	4	81–182	116	3	73–150	123

[a] Weights are means per pair from each animal.

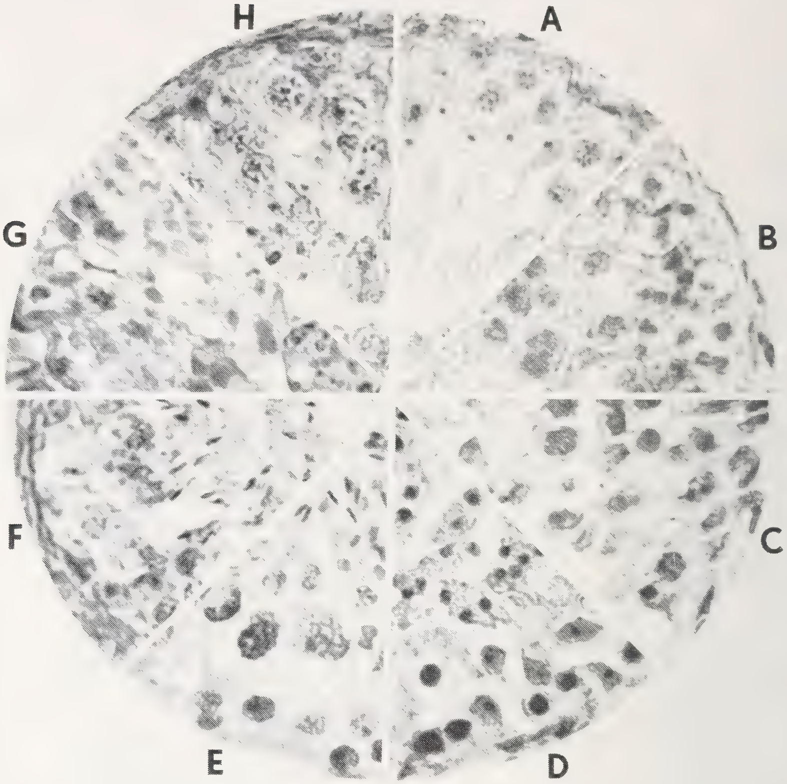


Fig. 113. Histological stages in the annual cycle of the seminiferous epithelium in testes of Pacific walruses. Associations: A, B, C, recrudescence; D, E, F, spermiogenesis; and G, H, retrogression. (Photos by F. H. Fay)

Association A.—Tubule diameter 114–146 μm; basement membrane 2–3 μm thick; epithelium 50–60 μm tall and composed of Sertoli cells and spermatogonia only. Initially, the spermatogonia are in a single cell layer adjacent to the basement membrane, and the chromatin granules of their nuclei are about intermediate in size between those of types A and B. In later stages, the nuclei are darkly stained and the cells more numerous, forming a generative epithelium 2 to 4 cells thick. This change could be due to proliferation of the "dormant" spermatogonia or, more likely, to contraction of the tubules associated with the general reduction in volume of the testis, for I saw no evidence of mitosis.

Association B.—Tubule diameter 76–148 μm; basement membrane 2–3 μm; epithelium 40–60 μm tall; spermatogonia nearly all type B and in several layers, later subsiding to a single layer with a few mitotic figures. Some primary and secondary spermatocytes present, but no spermatids; nuclei of the Sertoli cells becoming indistinct.

Association C. —Tubule diameter 105–153 μm; basement membrane 3–5 μm; epithelium 50–60 μm tall. Spermatogonia mostly like type A; primary and secondary spermatocytes abundant; nuclei of the Sertoli cells mostly indistinct. This is a state of rapid proliferation, before spermiogenesis.

Association D. —Tubule diameter 128–200 μm; basement membrane 7-8 μm; epithelium 50–80 μm tall. Spermatogonia mostly type B; Sertoli cells indistinct; spermatocytes less numerous than in *C*; round spermatids abundant.

Association E. —Tubule diameter 156–223 μm; basement membrane 5 μm; epithelium 50–80 μm tall. Spermatogonia mostly type B; Sertoli cells indistinct; spermatocytes and oval to elongate spermatids abundant, the latter occurring in clumps near the margin of the lumen.

Association F. —Tubule diameter 131–232 μm; basement membrane 2–3 μm; epithelium 60 μm tall. Spermatogonia mostly type A. Spermatocytes more abundant than in *E*; immature (round-oval) spermatids scarce. A few clumps of mature spermatids at the margin of the lumen; spermatozoa abundant in the lumen. A few cell fragments, apparently from degenerating spermatids, also are in the lumen.

Association G. —Tubule diameter 131–211 μm; basement membrane 5 μm; epithelium 50 μm tall. Spermatogonia mostly type A; Sertoli cells distinct; all ranks of germ cells degenerating and progressing toward the lumen. In the lumen are numerous spermatid giant cells, some with as many as 30 nuclei.

Association H. —Tubule diameter 115–160 μm; basement membrane 3 μm; intact epithelium about 30 μm tall. Spermatogonia mostly type A; Sertoli cells distinct. A few degenerating spermatogonia near the lumen have very large, granular nuclei. The lumen contains a few spermatocyte giant cells and masses of cellular debris. Spermatids are absent.

In this analysis of the annual histological cycle in the testes, the period of recrudescence is considered to begin with association *A* and end with *C*; spermiogenesis extends from *D* to *F*, and retrogression from *G* to *H*. The complete cycle is continuous; each association grades into the next, and the occurrence of any association never was synchronous in all of the tubules of a testis.

Each specimen was classified according to the cellular association represented in most of its seminiferous tubules. The results, when ranked by age and month of collection (Table 29), suggest that the timing of onset of spermiogenesis is more erratic in the adolescent and subadult age classes than it is in the adults, and that the period of potency tends to be, usually, 1 to 2 months later in the adolescents and subadults than in the adults. Most mature adults, 15 years old and older, were potent from November to March, whereas the subadults (10–14 years) were potent mostly from December or January until May. An age-related difference in seasonal development of the testes was evident also in their weight (Fig. 114) and in the comparative size of their seminiferous tubules. In general, the annual peak of development in tubule size and weight of the testes seemed to occur in February–March in the adolescent and subadult males, and in December–January in the adults.

These findings correspond to those of other investigators. Mansfield (1958*a*) reported that one adult taken in November and one in March were potent, whereas none of 30 taken in June to October was potent. Gol'tsev (1978) found that, in 115 males taken in March and April, the 8- to 10-year-old animals were

Table 29. *Predominant cellular associations in the seminiferous epithelium of the testes of Pacific walruses, in relation to age and month of collection.*

Age class (years)	No. of specimens	Cellular associations per specimen per month[a]											
		Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
5–7	12	—	—	—	BB	BD	—	B	AG	—	AC	CD	B
8–9	10	—	—	—	BBBD	BB	—	—	G	F	GG	—	—
10–11	13	B	—	—	B	BBC	—	DE	—	F	FFF	—	B
12	12	—	—	—	BC	DDE	E	—	F	—	DFFH	—	B
13–14	13	B	—	—	CC	CDDEE	—	E	—	—	EFFA	—	—
15–16	19	B	—	—	E	DDDDE	C	—	G	F	FGHA	AA	BBB
17–18	8	BBB	—	—	E	DDE	—	—	E	—	—	—	—
19–22	15	ABB	—	—	—	D	E	—	GH	A	FGGH	A	BB
23–37	12	—	—	—	—	D	E	E	E	AAA	GGHH	A	—

[a]Each letter represents one specimen: A, B, C = recrudescence; D, E, F = spermiogenesis; G, H = retrogression.

Table 30. *Frequency of occurrence by month of spermatozoa in the corpora epididymides of Pacific walruses in relation to age.*

Age class (years)	No. per month of animals with spermatozoa in the epididymis/no. examined											
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
5–9	—	—	—	0/5	0/6	—	0/1	0/3	—	0/1	—	0/1
10–13	0/1	—	—	0/3	1/9	1/1	3/3	1/1	—	1/4	—	0/2
14–37	0/5	—	—	2/3	9/14	1/3	1/1	2/5	—	2/8	0/4	0/5

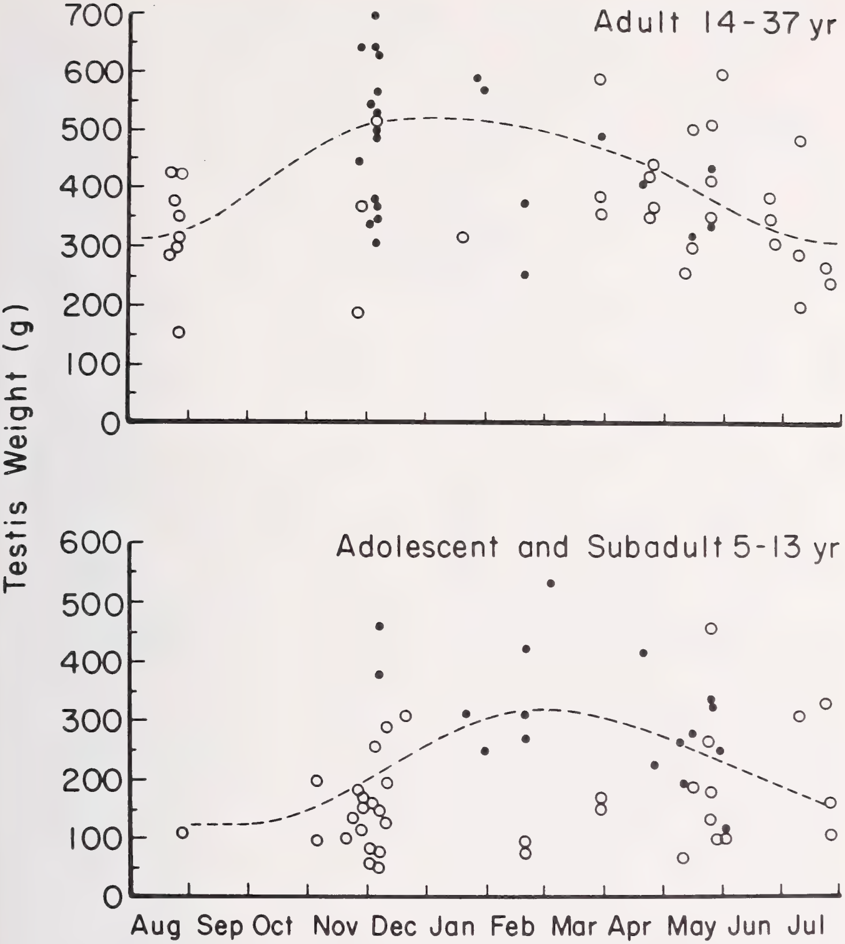


Fig. 114. Weight of the testes per month in adult and adolescent and subadult Pacific walruses. Each point represents the mean of the pair from one animal and indicates histological findings of spermiogenesis (dots) versus recrudescence or retrogression (circles). Curves were fitted visually.

in "beginning stages" of spermiogenesis; the 11- to 19-year-old subadults and young adults were spermiogenetic; and the older adults (up to 32 years) showed signs of retrogression. Krylov (1967) observed that animals 10 to 15 years old taken in April to June were potent, but the older adults were not. Of 712 males examined by Krylov (1969) from July to October, only 1 (on 26 July) was potent.

I found spermatozoa in the corpus epididymis mainly of animals that were 14 years old or older and principally from November to March (Table 30). In animals 10 to 13 years old, spermatozoa were present less frequently and somewhat later (December to May); I found none in specimens less than 10 years old.

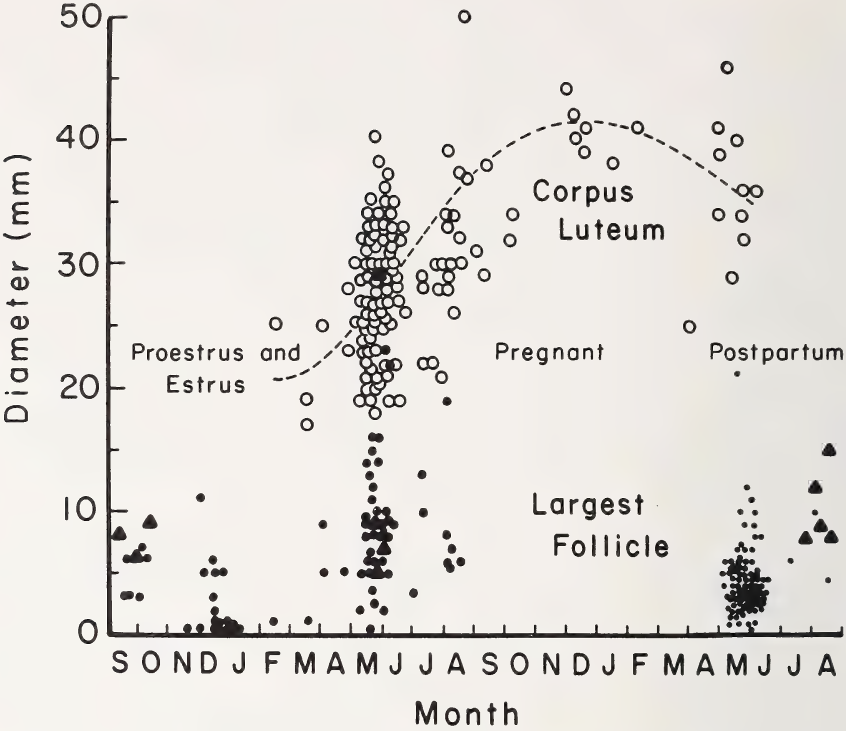


Fig. 115. Diameters of the largest healthy (dots) or degenerate (triangles) follicles and of the corpora lutea (circles) in ovaries of adult walruses, in relation to date of collection. Each point represents one specimen. Curve was fitted visually. (From J. J. Burns, F. H. Fay, and A. W. Mansfield, unpublished data).

Ovarian Cycle

One of my objectives in this study was to obtain monthly series of ovaries from adult females, in order to determine the time when most ova are shed and fertilized (i.e., the mating season). The data obtained, together with those provided by Mansfield (1958*a*) and by J. J. Burns (personal communication), are represented graphically in Fig. 115.

Follicle size in the nonpregnant, potentially estrous animals taken in September to December suggests a slight trend of increase during that period, but only one animal on 6 December had a healthy follicle 11 mm in diameter that appeared to be ripening. Regrettably, very few potentially estrous specimens were obtained in mid-December to April, and those few did not show any ripe follicles. The occurrence of new corpora lutea of pregnancy as early as mid-February and March, however, indicates that ovulation had begun during the winter. Ripe or ripening follicles were present in some individuals as late as July and August, long after most of the metestrous females had a well-developed corpus luteum and were in their second trimester of pregnancy.

The earliest corpus luteum (14 February) was 25 mm in diameter and had a prominent, incompletely healed ovulation scar in the adjacent tunic. About three-fourths of the corpus was luteinized; the portion that was not luteinized contained several fluid-filled cavities. Three unruptured follicles 8 to 12 mm in diameter that were adjacent to it also were partly luteinized (accessory corpora). In histological section, the lutein cells of the ruptured follicle were round to oval, 13 to 19 μm in diameter, mostly with rather oval to oblong, darkly stained nuclei, mostly with no distinct nucleoli. The cytoplasm appeared "frothy" with secretion droplets and lacked vacuoles (Fig. 116*a*).

Of 27 specimens obtained in March and April, 20 (74%) already had a firm, well-formed corpus luteum. The other seven had follicles up to 9 mm in diameter. The corpora lutea in each of the 20 specimens were rounded and contained no fluid-filled spaces or hemorrhage; they ranged in diameter from 17 to 28 mm. Histologically, a specimen taken on 17 March showed lutein cells more rounded than those in the February specimen and slightly larger (17 to 25 μm); the large nuclei were rounded to oval, mostly with a prominent, darkly staining nucleolus (Fig. 116*b*). The cytoplasm was frothy, with no vacuoles, and there was a remarkably large amount of interstitial vascular development. The corpus from one taken on 1 April had somewhat larger lutein cells, 17 to 33 μm in diameter. These differed from the foregoing in having numerous large vacuoles up to 19 μm in diameter and indistinct nucleoli (Fig. 116*c*).

Of 154 specimens taken in May and June, 105 (68%) already had ovulated. At least 10 of the others had ripe or ripening follicles larger than 10 mm in diameter. The largest of those follicles (29 mm in diameter) was degenerate, as indicated by its milky liquor folliculi. In the 105 specimens that already had ovulated, the corpora lutea of pregnancy were well developed and grossly resembled those from the March–April specimens, but they were mostly somewhat larger (18 to 40 mm). Three of these were examined histologically. The first, from an animal taken on 30 May with a 0.7-mm unattached blastocyst in the uterus, had lutein cells that were larger (31 to 45 μm) and more rounded than in any of the foregoing. These cells contained an abundance of vacuoles up to 20 μm in diameter (Fig. 116*d*). The nuclei also were large and rounded to oval, with a prominent, usually peripheral nucleolus. The second corpus, from an animal taken on 22 May with a 6-mm elliptical blastocyst, was similar to the first, except that the lutein cells were slightly larger (33 to 48 μm). In the third corpus, from an animal taken on 10 June with a newly implanted embryo, the cytoplasm of the lutein cells was somewhat finer-grained, and the nucleoli were more often central than peripheral (Fig. 116*e*). The lutein cells in this corpus were larger than those in any of the foregoing (37 to 58 μm in diameter).

Of 23 specimens taken in July and August, 14 (61%) had a large corpus luteum of pregnancy; a few had corpora atretica, and 2 had ripe follicles up to 13 and 19 mm in diameter. I did not examine the corpora lutea of any of these histologically.

The corpora lutea of specimens taken during the autumn and winter tended to be still larger (Fig. 115). Judging from histological examination of two of those corpora from animals taken on 30 November and 8 February, there is gradual fibrous infiltration of the corpus throughout the winter and some diminution in size of the lutein cells. In the November specimen, the lutein cells ranged in

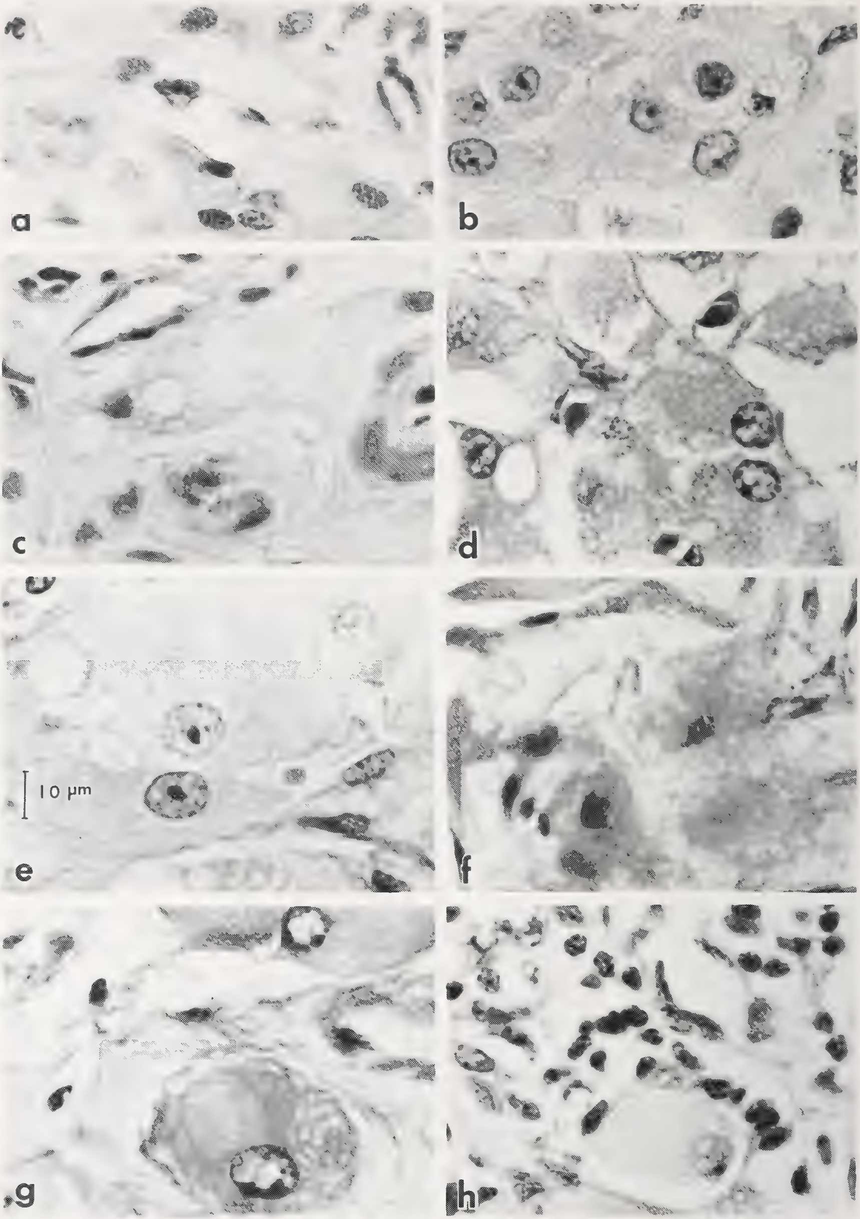


Fig. 116. Comparative histological characters of corpora lutea at different stages of pregnancy in Pacific walruses: (a) during initial luteinization of a recently ruptured follicle (14 February); (b) in a 17-mm, fully luteinized corpus (17 March); (c) in a 25-mm corpus (1 April); (d) in a 27-mm corpus from a female with a 0.7-mm unimplanted blastocyst (30 May); (e) in a 32-mm corpus, postimplantation (10 June); (f) in a 44-mm corpus, about halfway through gestation (30 November); (g) in a 35-mm corpus at full-term (24 May); and (h) in a 33-mm corpus, immediately postpartum (12 May). (Photos by F. H. Fay)

diameter from 25 to 41 μm, and their nuclei were more diffused than in the earlier specimens, with no distinct nucleolus (Fig. 116*f*). Diameters of lutein cells in the February specimen were 20 to 31 μm. In both of these specimens, the cytoplasm had taken on a coarser, more granular appearance, and large vacuoles were scarce.

In specimens taken during late winter and spring, fibrous invasion of the corpora was evident macroscopically, as was the reduction in size from the autumn–winter maximum. I examined two such corpora histologically. The first, from a specimen with a full-term fetus taken on 24 May, showed virtual isolation of some lutein cells by the surrounding fibrous tissue (Fig. 116*g*). The cells were large and more rounded than in winter specimens, with a coarse, granular cytoplasm containing few vacuoles. The nucleus also was large and round, and the nucleolus darkly stained and peripheral. Lutein cell diameters ranged from 25 to 45 μm. The second corpus, from a specimen taken on 12 May with a calf no more than a few hours old, was essentially the same as in the 24 May specimen, except that it showed extensive thecal invasion, as well (Fig. 116*h*). The corpora in two animals taken on 3 and 22 May, with calves judged to have been at least 1 week old, were comparable histologically to the 12 May specimen.

The largest follicles in the ovaries of postpartum females tended to be mostly less than 5 mm in diameter during the first weeks after birth. By late May and June, however, there was a trend of increase in follicle size, probably to a maximum in July or August. Most of those larger follicles were degenerate; apparently none had ruptured during this postpartum estrus.

Time of Mating

Several investigators have estimated that the mating of walruses occurs in the spring, at various times from mid-April to July (Chapskii 1936; Collins 1940; Brooks 1954; Mansfield 1958*a*; Krylov 1962). Those estimates were based mainly on comparative embryonic development, rather than actual evidence of ovulation, and were made with the assumption that in the walrus there is no delayed implantation. More recently, Krylov (1966*b*) indicated that the mating period is from March to July, but his basis for that statement was not made clear. Subsequently, he (Krylov 1966*c*) declared that most of the mating occurs in May and June. Still later, Krylov (1969) placed mating in late April to early June, in the same period as birth.

In the reproductive cycles of other pinnipeds, insofar as they are known (see reviews by Harrison et al. 1952; Harrison 1969), the principal period of mating seems always to be about 2 to 3 months long and to begin about the time of the peak in size of the testes of the adult males. By analogy, the mating season of the Pacific walrus would be in January to February, rather than in April to June. In April to June, the testes of nearly all of the adult males already were in a state of retrogression.

As a whole, the findings presented here suggest that estrus in some walruses may take place as early as December or as late as August. This should not be regarded as indicative of a 9-month-long mating season, for the data from the males indicate that mature adults are fertile mainly from December to March. Hence, it is probable that most fertilizations take place in the winter period. Of the 14 potentially estrous females taken in February and March, 10 (70%)

Table 31. *Frequency of occurrence of corpora lutea of pregnancy in ovaries of "potentially estrous"[a] females taken in the Bering and Chukchi seas from November to August.*[b]

Month	No. of specimens	No. with corpus luteum of pregnancy	Percent with corpus luteum of pregnancy
November	1	0	0
December	13	0	0
January	3	0	0
February	2	1	50
March	12	9	75
April	15	11	73
May	98	65	66
June	56	40	71
July	9	3	33
August	14	11	79

[a] Not carrying a near- or full-term fetus (November to June) and not having born a new calf (April to August).

[b] Data from Gol'tsev (1978 and unpublished data) and J. J. Burns and F. H. Fay (unpublished data).

already had a large corpus luteum of pregnancy; by April and May, that proportion had not risen, and it apparently did not change thereafter (Table 31).

The condition of the earliest recorded corpus luteum in a female taken on 14 February, relative to that of corpora lutea in other pinnipeds and other carnivores (Wimsatt 1963; Harrison 1963; Craig 1964; Harrison and Weir 1977), indicated that ovulation had occurred 2 to 4 weeks earlier, in mid-January to late January. The comparative condition of those in females taken in March suggested that ovulation had occurred at least 1 month earlier. Conversely, the corpora lutea in females taken in April to June were mostly much larger than those in February to March, and their histological condition was consistent with that of corpora in other pinnipeds at the time of implantation (cf. Craig 1964). Whereas some females may ovulate later than February, I suspect that they mostly fail to be fertilized.

Breeding Behavior

Because the mating season of walruses previously was thought to be in April to June, at the same time as calving (Allen 1880; Chapskii 1936; Belopol'skii 1939; Nikulin 1941; Freiman 1941; Brooks 1954; Krylov 1969), most of the observations thought to be relevant to breeding behavior were made at that time. In retrospect, it is not surprising that the observers saw no remarkable social organization, for most of the herds in spring are made up either of subadult and adult males or of adult females with their dependent young. Mixed herds of adult males and females, such as might be expected to occur commonly during the mating season, are conspicuously scarce to absent at that time (Nikulin 1941).

Hanna (1923) apparently considered that the large herds found on certain islands in the Bering Sea in summer were "breeding rookeries," comparable to those of fur seals and sea lions; the same opinion was expressed by Scheffer (1950). Elliott (1875) apparently was confused by this when he found that the herd on Walrus Island, Pribilof Islands, was made up only of males. Furthermore, he was told by the Aleut inhabitants of that area that females never joined that herd. Dall (1902), in a less conservative mood, interpreted this masculine group as "an assembly of peculiar character . . . entirely composed of old males driven away from the herds by the competitive valor of their younger and more active congeners, and forming a sort of old gentlemen's club, existing in torpid dignity away from an atmosphere of irritating disrespect." The more recent work of Bel'kovich and Yablokov (1961), Yablokov and Bel'kovich (1963), Gol'tsev (1968), and Miller (1975*a*, 1976) has fully confirmed that such herds are composed only of males and that they contain not only adults but subadults and juveniles as well.

Belopol'skii (1939), Freiman (1941), Nikulin (1941), and Brooks (1954) predicted that small, loosely organized "harems" are formed on the ice in spring, and that these are very transient because of the rapidly changing ice conditions. However, they saw no such groups and produced no other supporting evidence for their predictions, apart from reiteration of the fact of sexual dimorphism and analogy with the Otariidae. Probable cases of coition were reported by Mansfield (1958*a*) in April, by A. V. Yablokov (personal communication) in "spring," by R. A. Ryder (personal communication) in May, by Brooks (1954) in May, June, and July, by Johansen (1912) in August, by Freuchen (1935) in September, and by the St. Lawrence Islanders (personal communication) in November. However, in none of those reports was any mention made of social organization, other than that a male and female were together.

Some investigators have predicted that walruses are monogamous (Allen 1880; Nutting 1891; Bertram 1940; Popov 1960*a*; Krylov 1968), rather than polygynous. The principal basis for that prediction seems to have been that some very small, mixed groups, resembling families do occur, especially where remnant populations have survived, for example in the fjords of East Greenland and about the islets of the Svalbard area (see Pedersen 1962). However, "family groups" containing an adult pair (bull and cow) certainly are the exception rather than the rule in the Bering–Chukchi region.

Walruses in captivity seem to copulate in all months of the year, perhaps more often in spring than at other times and certainly more often in than out of the water (E. D. Asper, D. H. Brown, and G. C. Ray, personal communication). During the period January to March, when most of the mating by free-living walruses probably takes place, the animals tend to be well out in the pack ice, remote from shore and not readily accessible for observation. Only a small amount of information has been obtained on their behavior during that time (Ray and Watkins 1975; F. H. Fay, G. C. Ray, and A. A. Kibal'chich, unpublished data), which may be summarized as follows.

In most winters, nearly all of the adult females and young are situated in the St. Lawrence and Bristol Bay concentration areas. There, the potentially estrous females (i.e., those not carrying a near-term fetus) congregate in herds, each of which is attended by one or more large adult bulls. When those herds of females and young are at rest (on the ice or in the water), the bulls station themselves in the water alongside the herd, where they perform visual and acoustical displays.

Each display lasts for 2 to 3 min, and consists of a subsurface portion, in which series of pulses ("clicks" or "knocks") and bell-like sounds are made (Ray and Watkins 1975), and a surface portion, in which the bull raises his head above the water and emits a series of sharp "clacks" (apparently with his teeth) and a short, harsh whistle. Each adult bull in the water adjacent to the herd of females performs these displays continuously, for as long as the females remain at rest. Presumably, the displays serve as advertisement to the females of the male's sexual readiness and as a deterrent to other males in the vicinity. We saw females leave the herd and join a displaying male in the water. After some preliminary play (nuzzling, mounting), they dove beneath the surface, where copulation may have taken place.

When more than one bull was attending a herd of females, the bulls maintained a distance of about 7 to 10 m apart, and each performed his displays in a fixed location. Invasion of a male's display locus by another male resulted, first, in visual agonistic displays similar to those described by Miller (1975*a*), then in violent fighting. The "winner" of the ensuing battle continued to display in the same locus; the "loser" retreated. We frequently saw bulls with bleeding wounds, which suggested that the fights between bulls often result in physical injury to one or both of the combatants.

The sex ratio of males to females of breeding age in the two main wintering areas where those observations were made ranged from 1:5 to 1:17 in March and April (Table 1). The ratio of displaying males to potential mates, however, ranged from 1:5 to 1:67 (average, about 1:23). Subadult and adolescent males were scarce to absent in the vicinity of the displaying bulls. The few that were seen were situated within rather than at the periphery of the female herds and were engaged only in sleeping or feeding, not in displays. One of these, 6.8 years old, was taken on 21 March and found to be impotent and infertile.

I sighted herds of females attended by one or more displaying bulls often in March, infrequently in early April, and not at all after that time. Of some 200 groups of females in mid-April to mid-June, none was comparable to the mating groups seen in March, inasmuch as none contained a displaying male.

The mature bulls that I saw in March and early April mostly hauled out separately. After the mating season, however, mature bulls form all-male herds, many of which resort in large numbers to hauling grounds, such as Round Island and Rudder Spit, where they simply rest, heal their wounds, and molt. Probably, Round Island (and formerly, Walrus Island in the Pribilof area) is the traditional summer haven for males of the Bristol Bay wintering concentration; the Rudder, Meechken, and Arakamchechen hauling grounds along the Soviet coast probably are the traditional summering areas for males from the St. Lawrence concentration. That is, the all-male herds found on the Bering Sea hauling grounds in summer probably are not outcasts or "old gentlemen's clubs" so colorfully reputed by Dall (1902), but are made up of most of the mature, breeding males from the winter concentrations.

Pregnancy

Within a few days after fertilization, the mammalian ovum becomes a fluid-filled, spherical vesicle, the blastocyst. In some mammals, the embryo may remain in that stage for some months, before continuing its development. Although many of the walruses taken in March and April (and many in May and June, as well) had a large, well-developed corpus luteum, most had no visible embryo in the uterus (Brooks 1954; Burns 1965; Krylov 1969). These animals have been assumed to be pregnant, with the embryo still in the blastocyst stage. I investigated this in two females, taken on 14 and 30 May. By saline perfusion of the lumina of their uterine horns, I was able to isolate the blastocysts, which were 0.4 and 0.9 mm in diameter, respectively (Fig. 117*a*).

Time of Implantation

The rate of growth of the mammalian conceptus is inversely proportional to the length of the gestation period, from nidation (implantation) to birth. Thus, the size of the fetus at any instant in its development, relative to the size at birth, is indicative of the amount of gestation completed and to be completed. In many species of mammals, the length of the embryo at the time of its attachment to the uterine wall is about 3 to 4% of the crown–rump length at birth (Cloete 1939; Winters et al. 1942; Patten 1953), at which size it is in the neurula stage (Evans and Sack 1973). By analogy, the length of the embryonic Pacific walrus at implantation would be about 3 or 4 cm, and the time of implantation would be in late June to late July. My findings and those reported by Belopol'skii (1939), Collins (1940), Brooks (1954), Krylov (1966*b*, 1969), and J. J. Burns (unpublished data), lend support to that prediction (Table 32).

Embryos large enough to be distinguished without magnification were identified first in 2 of 70 females taken on 22 and 25 May with a well-developed corpus luteum of pregnancy. Each embryo was an elliptical blastocyst, 6 × 4 mm in diameter, in which the blastoderm (about 3 mm long) was in the primitive streak stage of development (Fig. 117*b*). Two other blastocysts in this condition were recovered from animals taken on 2 June and one other from a female taken on 7 June. Although there was no gross evidence that these elliptical bodies were attached to the endometrium, I assume because of their size and shape that they were in an initial stage of nidation (cf. Mayer 1963).

Table 32. *Frequency of occurrence per month of unattached blastocysts and of implanted embryos and fetuses in Pacific walrus females having a corpus luteum of pregnancy.*[a]

	Unattached blastocyst		
Month	Not visible	Visible	Embryo implanted
February	1	0	0
March	9	0	0
April	11	0	0
May	68	2	0
June	38	3	7
July	0	1	9
August	0	1	23
September	0	0	78

[a] Data from Krylov (1966*b*, 1969) and J. J. Burns and F. H. Fay (unpublished data).

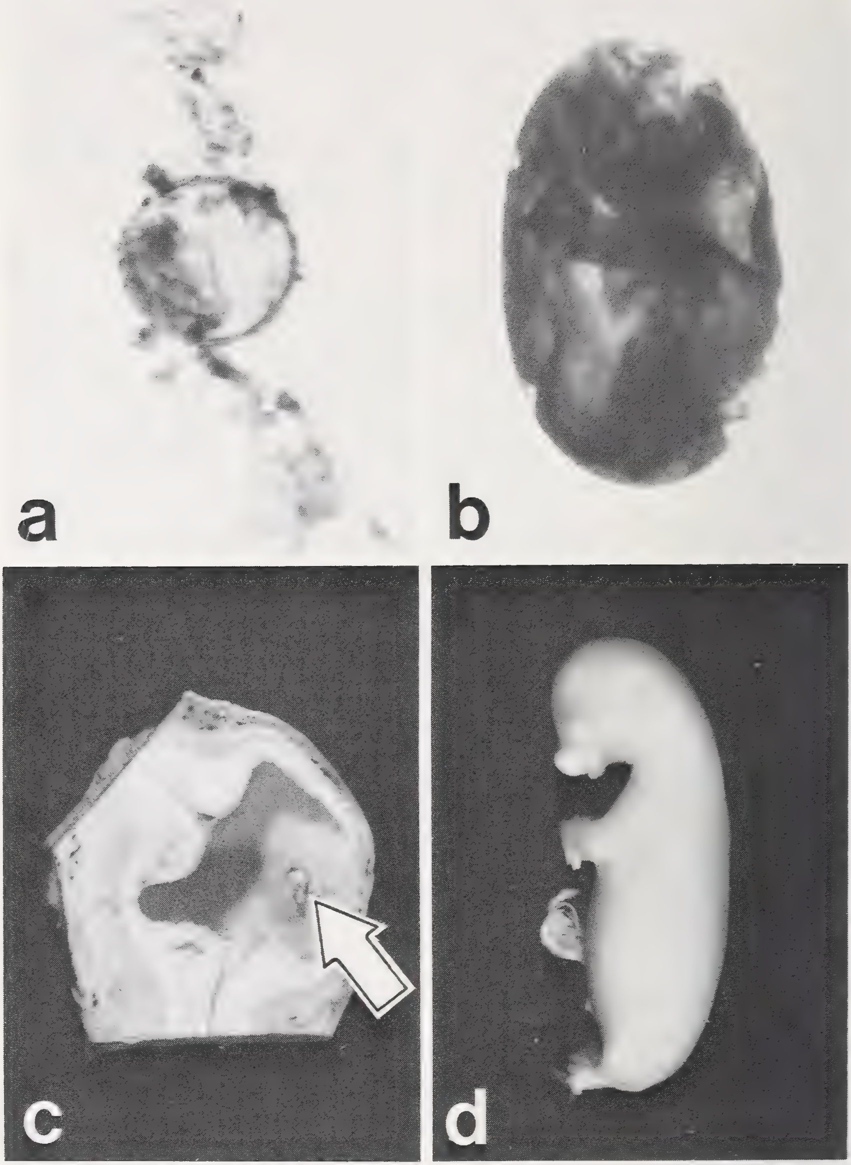


Fig. 117. Examples of embryos and fetuses of Pacific walruses: (a) 0.4-mm free blastocyst from a female taken on 14 May; (b) 6.1-mm elliptical blastocyst in the primitive streak stage, early in nidation (25 May); (c) 7-mm newly implanted neurula (arrow) in the uterus (17 June); and (d) 61-mm fetus (20 July). (Photos by F. H. Fay)

Three implanted embryos, 5, 23, and 16 mm long, were found by Brooks (1954) in females taken on 10, 15, and 16 June, respectively; J. J. Burns (unpublished data) recovered a 7-mm implanted embryo from a female taken on 17 June (Fig. 117*c*). Another of Burns' specimens, taken on 1 June, showed local swelling of one uterine horn, suggestive of implantation (cf. Wimsatt 1963), but the embryo was not certainly identified. Krylov (1969) reported the finding of implanted embryos 7 and 9 cm long in two females taken on 13 June.

Belopol'skii (1939) and Collins (1940) found implanted embryos and fetuses in several females during July but did not indicate whether they examined other females without finding any embryos. Krylov (1969) reported six implanted embryos 13 to 25 cm long (nose–tail length) from females taken on 2 and 20 July; earlier (Krylov 1966*b*), he reported another female in July with an unimplanted blastocyst. All but 1 of 102 pregnant females examined by Krylov (1969) in August and September contained implanted fetuses. The one exception, taken on 31 August, contained a blastocyst comparable in size to that in an animal taken on 2 June.

The foregoing data indicate that nidation may begin as early as May or as late as July. In most females, however, implantation of the blastocyst seems to take place during June and July. The modal time of implantation probably is about 1 July, 4 to 5 months after the probable modal time of ovulation and fertilization. During those months, the spherical, microscopic blastocyst evidently remains in an unattached state of suspended development.

Until recently, delayed implantation had been assumed not to take place in walruses (Scheffer 1958; Asdell 1964), though the possibility of its occurrence was not overlooked by Burns (1965) and Harrison (1969). By addition of this 4-to 5-month period of delayed implantation, the duration of pregnancy in the walrus now appears to be at least 15 to 16 months, rather than 11 to 12 months as previously believed. Such a long duration is unusual among mammals (Asdell 1964) and may be unique among pinnipeds, or matched only by the Australian sea lion, *Neophoca cinerea* (Ling and Walker 1978).

Growth of Fetus

The growth of the fetal Pacific walrus is depicted in Fig. 118, on the basis of data compiled from various sources. Measurements of embryos and fetuses reported in the literature have been expressed in several different forms: (1) nose–tail length along the curvature of the back, with the animal in the normal fetal position; (2) standard length from nose to tail (straight line), with the animal lying on its back and with head and tail extended; and (3) crown–rump length, in a straight line from top of head to base of tail, with the animal in the normal fetal position (Fig. 119). Since crown–rump length usually has been found most reliable for analysis of fetal growth (Harvey 1959; Evans and Sack 1973), I converted all of the available nose–tail and standard length measurements to crown–rump length, based on comparative measurements of 16 specimens examined by Belopol'skii (1939) and me, as follows:

$$\text{Crown–rump L} = 56\% \text{ nose–tail L} = 84\% \text{ standard L}$$

The resultant estimated crown–rump lengths, although only approximate, are comparable in magnitude to those from actual measurements of specimens

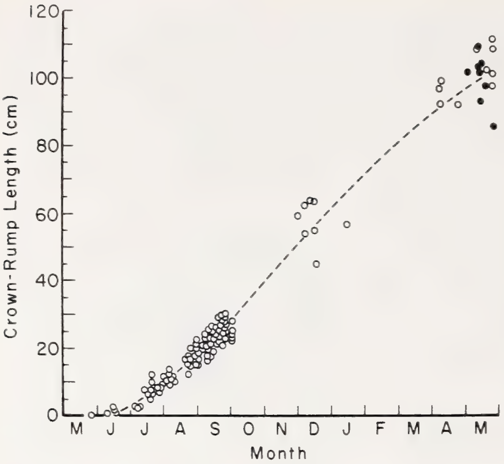


Fig. 118. Crown-rump lengths of Pacific walrus embryos and fetuses (circles) and newborn calves (dots), in relation to time of collection. From data of Belopol'skii (1939), Krylov (1969), and J. W. Brooks, J. J. Burns, and F. H. Fay (unpublished data). Curve was fitted visually.

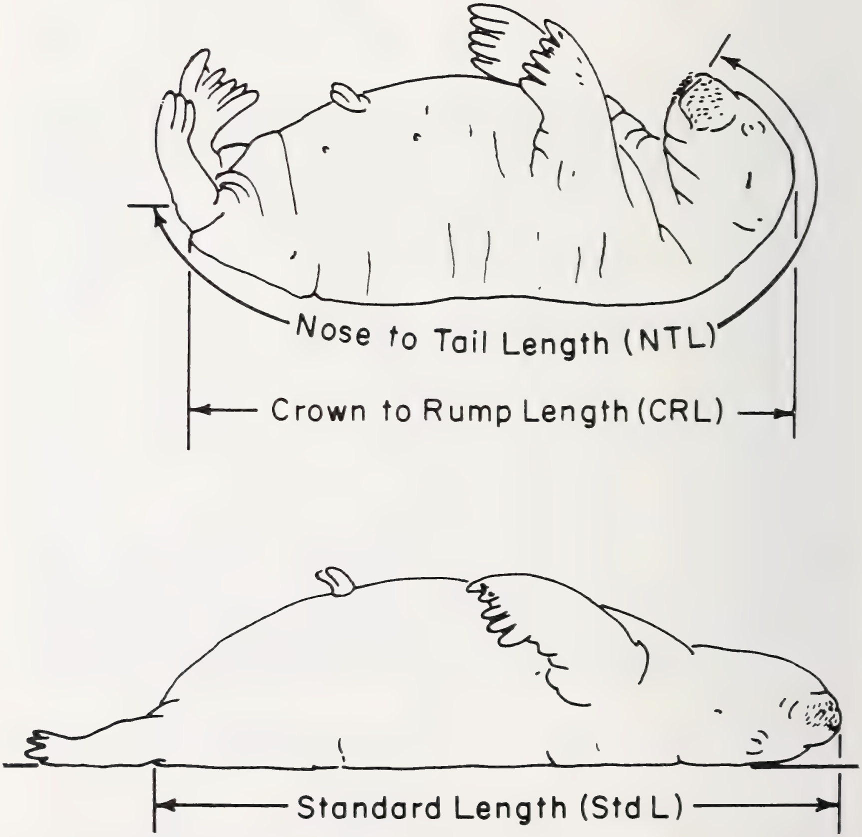


Fig. 119. The three methods of measurement used for describing the growth of walrus fetuses.

drawn from other populations at the same time of the year, for example by Chapskii (1936) and Mansfield (1958*a*).

The indicated mean crown–rump length at birth, based on 15 full-term fetuses and newborn calves taken between 24 April and 26 May, is about 101 cm (range, 92 to 112 cm). The mean standard length at birth is about 113 cm (range, 95 to 123 cm).

In each of the pregnant and postpartum females in my sample, the embryo, fetus, or new placental scar was in the uterine horn adjacent to the ovary with the corpus luteum. Transuterine migration of an ovum or blastocyst to the opposite horn probably is not possible in the walrus because of the didelphic structure of the uterus. The complete separation of the right and left uterine horns affords no inter-cornual passage for the ovum or unimplanted embryo, other than through the abdominal cavity or the vagina, neither of which is a likely route. There are no records of ectopic, bursal, or oviductal pregnancies in the walrus.

Fetal Sex Ratio

Of 213 embryos and fetuses, most of which were obtained in June to November, 103 (48.4%) were males (Table 33). Conversely, of 395 calves, ranging in age from newborn to about 3 months old, 204 (51.6%) were males. Although neither of these proportions differs significantly from a 1:1 sex ratio, they suggest that there is a slightly higher proportion of females than of males in the fetal population and a higher proportion of males at birth.

Table 33. *Comparative numbers of male and female walrus fetuses and calves.*[a]

Life stage, and months	Males	Females	Total
Fetuses			
June–August	21	23	44
September–November	64	66	130
December–February	6	2	8
March–May	12	19	31
Total	103	110	213
Calves			
April–July	204	191	395

[a] Sources: Belopol'skii (1939), Nikulin (1941), Brooks (1954), Mansfield (1958*a*), Loughrey (1959), Krylov (1962, 1969), and J. J. Burns and F. H. Fay (unpublished data).

Time of Birth

The time of birth of walrus calves is generally regarded as being in May (Asdell 1964; Harrison 1969), but as Krylov (1969) has pointed out, there are few substantive data on that point in the literature. Belopol'skii (1939) recorded one "apparently recently born" calf on 14 May. Nikulin (1941) encountered no females in the first half of May with a full-term fetus; he saw only calves that had been born some time earlier. Brooks (1954) noted that the calves he saw in May and June still retained a portion of the umbilical cord, which suggested that they had been born recently. He also recorded two females with full-term fetuses on

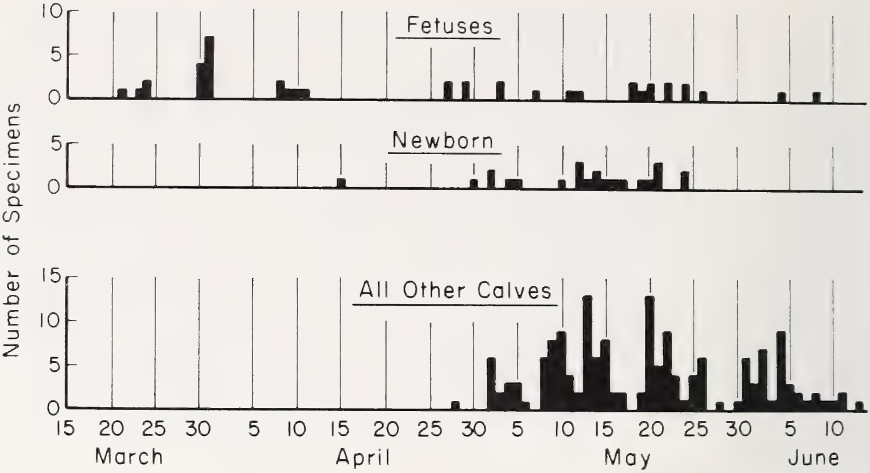


Fig. 120. Frequency of occurrence of near-term fetuses (upper), newborn calves less than 48 h old (center), and older calves of uncertain age (lower) during mid-March to mid-June. (From Brooks 1954, Krylov 1969, and J. J. Burns, F. H. Fay, K. W. Kenyon, and R. A. Ryder, unpublished data)

22 May. Krylov (1969) recorded six full-term fetuses between 8 April and 24 May and obtained the first newborn calves on 5 May.

During an aerial survey of the Pacific walrus population, Kenyon (1972) sighted and photographed a female with a calf, apparently just born (judging from blood on the floe), on 15 April. R. A. Ryder (personal communication) recorded a fresh ("steaming") placenta among a group of females and calves on the ice near St. Lawrence Island on 2 May and observed the birth of a calf on 21 May in the Chukchi Sea. Near St. Lawrence Island on 12 May, I examined a cow with new calf, together with the still-warm placenta and fetal membranes.

A graphic summary of all available data relating to time of birth is presented in Fig. 120. These findings indicate that (1) near- and full-term fetuses occur commonly as late as the last 10 days of May and occasionally in the first 10 days of June, (2) newborn calves, certainly less than 48 h old, occur commonly during late April and May, with the earliest record being 15 April, and (3) other, older calves have been recorded in abundance throughout May and June. The duration of the birth period implied by these data is about 55 days, from 15 April to at least 8 June, with a probable mode between 30 April and 25 May. From this, I estimate that the mean birth date is about 12 May.

Although most births take place from mid-April to mid-June, a few apparently occur at other times during the year. Freuchen (1935) reported two "newly born" calves taken in Frozen Strait, Foxe Basin, Canada, on 31 January, and Burns (1965) obtained a calf in Bering Strait in May that he judged had been born in January or February. I examined one calf in May that was unusually large and had a fully healed umbilicus, comparable in all respects to those taken in July by Nikulin (1941), hence I assumed that it might have been born as early as March. During an aerial survey flight on 1 March, K. W. Kenyon (1960*a*) sighted a small animal, possibly a newborn calf, in the midst of a group of cows on a bloody ice floe in the St. Lawrence concentration area. Instances of unusually late births were indicated by Tsalkin's (1937) finding of a full-term fetus in a cow taken at Franz Josef Land in July, a small calf possibly no more than a month old at Nunivak Island in November (T. E. Smith, personal communication), and the St. Lawrence Islanders' report to me of an animal taken in February that was comparable in size to those normally taken in November. The Thule Eskimos told Vibe (1950) that calves can be born in any season, probably meaning that births occasionally occur outside the normal spring season.

Newborn Calf and Its Environment

The calf at birth weighs about 63 kg. The placenta, which is about 35 cm wide and weighs about 6.8 kg, is expelled soon after the calf is born and is consumed by scavengers (mainly gulls), rather than by the mother. The calf is pale gray to gray-brown overall, with a dense, but very short and soft pelage. The naked areas on its appendages are of about the same pale color as the rest of the animal. A short remnant of the umbilical cord, up to 15 cm long, remains attached to the calf.

In the first days or weeks after birth, the calf not only grows larger and more robust but acquires a different coloration. The pelage takes on a reddish-brown to tawny hue, and the naked surfaces of the flippers become contrastingly dark, almost black. The remnant of the umbilical cord debrides, usually by late June or July (Nikulin 1941).

Single births are the rule. Twin fetuses have been recorded only three times (Nikulin 1954; Krylov 1962) in more than a thousand births recorded by Soviet and American investigators. There are no confirmed records of females successfully rearing twin calves.

Physical Conditions

In the season of birth, the Pacific walrus population is mainly concentrated in the northern end of the Bering Sea, in the vicinity of St. Lawrence Island and Bering Strait, and is in the course of its annual spring migration to the Arctic. Surface water temperatures there at that time are about −1.5°C, and the deteriorating winter pack ice covers from 30 to 80% of the area. Air temperatures range from about −20 to +10°C but are mostly in the range of 0 ± 5°C. High winds are infrequent, and severe storms with heavy precipitation occur less often than in any other season. In general, the weather in May and June is regarded by local inhabitants as some of the most pleasant and favorable of the year, although it is still relatively cool. Judging from the findings of Ray and Fay (1968), the thermal environment in air is mainly within the thermoneutral range for adult walruses but probably is somewhat cooler than the optimum (about 10 ± 5°C) for the calves. The suboptimal air temperature may be counterbalanced, however, by the frequent occurrence of fair weather at this time; solar radiation is near its maximum intensity and duration for the year.

Maternal–Neonatal Behavior

A brief account of the birth of a Pacific walrus calf was provided me by R. A. Ryder (personal communication), based on his observations from the icebreaker

Northwind in the southern Chukchi Sea on 21 May 1954:

> She [the cow] sat more or less upright on her front flippers with her body at right angles to the ship, distance approximately 300 yards. The posterior portion of her body was turned somewhat laterally with the ventral side away from the ship. When first seen, the calf was partly visible, steaming and wet appearing. As the ship continued to approach, the female squirmed occasionally and looked back at the newborn calf which gradually became more visible. It lay motionless for a minute or so until the mother saw the ship and slid into the brash. The parent promptly surfaced close by the floe and looked at the calf. It slowly wiggled to the edge of the floe and fell into the brash and water. The cow dived with the calf, [holding it] under her head and tusks. No sounds were heard from the cow or calf and no umbilical cord attachment or actual severing of same by the female was observed. A comparatively fresh afterbirth and another newborn calf were seen on the same floe.

A comparable first-hand account was related to me orally by one of the St. Lawrence Islanders.

Ryder also observed the presence of newborn calves and "fresh afterbirths (in at least one instance, still steaming)" on three occasions, and I saw the same twice. In each instance, the animals and placentas were on the ice, and there was a large amount of blood on the snow around them. For this reason, I assume that birth usually takes place on the ice, rather than in the water, though my basis for this judgment is admittedly weak. One probable record of birth in the water was reported to me by a group of Eskimos that had captured a cow with newborn calf in an ice-free area, at least 30 km from the nearest floe. They claimed to have had the swimming adult under observation for 15 to 20 min before the calf suddenly appeared before her in the water. The St. Lawrence Islanders stated that there had been very few previous sightings of births in the water.

All but 2 of about 22 full-term pregnant and newly postpartum cows that I saw in May and June were in semi-isolation, a few meters to 1 km from the nearest herd of cows with older calves. The two exceptions were cows with newly born calves on floes with more than 10 other adults and young. These observations suggest that the cow usually elects to be alone when it gives birth, rather than close to other animals. In none of the instances in my experience did a cow with a newborn calf have any other youngsters with it, though many of the near-term pregnant animals that I saw in March and early April were accompanied by 2- and 3-year-old young. This suggests that the near-term cow and her 2- or 3-year-old from the previous pregnancy usually separate in late April, just before the new calf is born.

Of eight cows with calves no more than 48 h old, only two were still at the site of birth; in those instances, birth had taken place only a few minutes before, judging from the warmth of the placenta. The Eskimos claim that the cow and calf usually move to another, "clean" floe within minutes after birth, presumably to free the calf of the fetal membranes and mucus and to avoid scavenging gulls (especially *Larus hyperboreus*) and fulmars (*Fulmarus glacialis*).

Cows with calves that were more than about 2 days old tended to congregate in herds, separate from the bulls and from all other females. These "nursery herds" (Burns 1970) sometimes consist of more than 200 animals, though herds of 20 to 50 are most common.

The social bond between mother and calf apparently is stronger in the walrus than in any other pinniped. The cows are highly solicitous of their offspring and are extremely protective, as noted earlier by many observers (e.g., see review by Allen 1880). The social bond is not "absolutely unbreakable" as Brooks (1954) supposed, but it seems to be unusual for a cow to become separated from her calf except under the most frightening circumstances. In some 50 encounters between Eskimos and walrus cows with young calves, I observed only six separations that resulted in the calves' being captured while the mothers escaped, apparently unharmed. On one occasion, a small herd was stampeded into the water, leaving behind an injured calf imprisoned in a smooth-sided crater in the ice. After a few minutes, one of the cows returned to the floe, emerged from the water, and approached the barking calf, even to within 2 m of the waiting hunters. This cow was shot, and the condition of her uterus, in regard to state of involution since parturition, seemed consistent with the state of development of the calf; hence, I presumed that she was its mother.

Burns (1965:32) observed that, when alarmed, "cows often pushed the calves into the water before entering themselves," and that the youngsters tended to be "herded" away by the older animals (Fig. 121). "The hollering of the calves can be heard at a considerable distance, and the older animals continue to return to the edge of the ice until the last of the noisy calves has been encouraged to leave." Lamont (1861:70,81,84) noted that the barking calves tend to attract other walruses.

Calves whose mothers had been shot usually remained with them and were easily captured by the hunters. Occasionally, a calf escaped into the water,

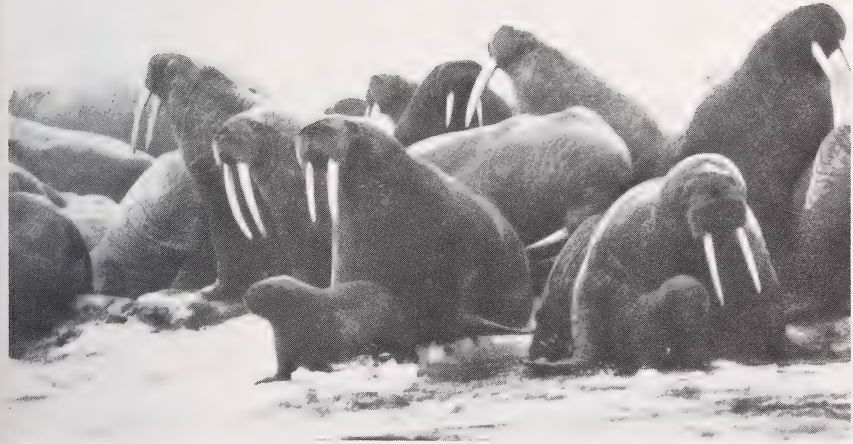


Fig. 121. A group of female Pacific walruses herding their calves into the water. (Photo by L. M. Shults)

where it swam about nearby, barking incessantly for some minutes thereafter. In those instances, the calf often was lured within the grasp of the hunters, apparently in response to imitation of the adults' barking. Orphaned calves sometimes are "rescued" by other walruses, who grasp them with their fore-flippers and carry them away (Bruce and Clarke 1899; Bel'kovich and Yablokov 1961). I witnessed three such "rescues" and was told of two others by reputable observers. In three instances, the calf was carried off by a subadult or adult male; in two others it was taken by an adult female. The probability of survival of those calves is questionable, but there is some evidence of fosterage. J. J. Burns (unpublished data) and I observed seven definite instances of calves that were at least temporarily "adopted" by other cows; the St. Lawrence Islanders (personal communication) and Eley (1978) reported two others. Burns' records were of three barren cows and one newly impregnated cow, none of which had given birth less than 1 year previously but each of which was accompanied by a young calf, no more than a few days or weeks old. My records were of one cow containing a dead, partly autolyzed fetus but accompanied by a living calf, obviously of other parentage, and two in which the uterus had just begun to involute from parturition not more than 48 hours previously but were accompanied by calves that were certainly several weeks old. The Islanders report was of another cow with dead fetus and accompanied by a living calf. Eley's record was of a cow with a normal fetus and new calf, not her own. Unfortunately, neither Burns, Eley, nor I determined whether any of these adopted calves were being suckled by their foster parents. At least, none could have been considered "starvelings," inasmuch as they were not weakened or deficient in blubber relative to other, normal calves taken at the same time.

Postpartum Involution of Uterus and Corpus Luteum

The uterine horn of pregnancy rapidly diminishes in size, probably reaching its normal progestational length within about 2 months after birth (cf. Gier and Marion 1967). Apparently, a low amplitude, annual cycle of uterine size is established thereafter, even in the absence of further pregnancies (Fig. 122).

The corpus luteum undergoes a significant reduction in volume about the time of parturition. In specimens taken 2 months after birth, it was no more than half as large as the corpus luteum of pregnancy (Fig. 123) and was made up mostly of fibrous tissue; lutein cells were scarcely evident. The corpora albicantia of females about 7 months postpartum seemed to be entirely of grayish connective tissue, typically having a stellate organization. The stellate structure was apparent in some instances up to 2 years after parturition. Corpora albicantia 3 years old and older were more consolidated and whitish, with no apparent stellate organization.

Evidently the rate of diminution in size of the corpora albicantia from pregnancies varies widely. Some declined to less than 10 mm in diameter within 2 years, but others were nearly 20 mm in diameter after 3 years (Fig. 123).

Reproductive Performance

Rate of Ovulation

The age-specific fertility rate of 205 individuals in which the age at first

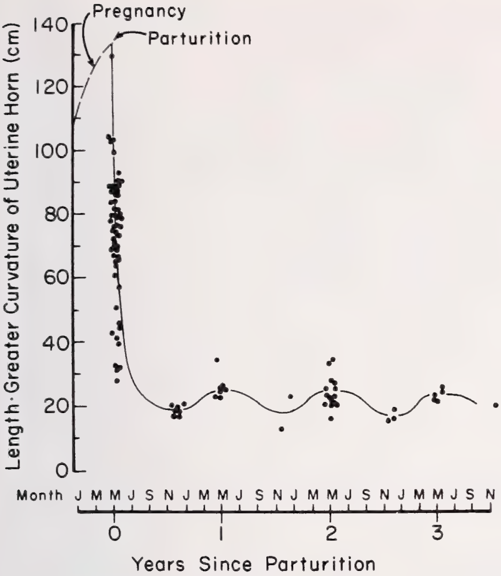


Fig. 122. Postpartum decrease in length of the uterine horn of pregnancy and the suggested subsequent annual cycle of uterine size. Curve was fitted visually.

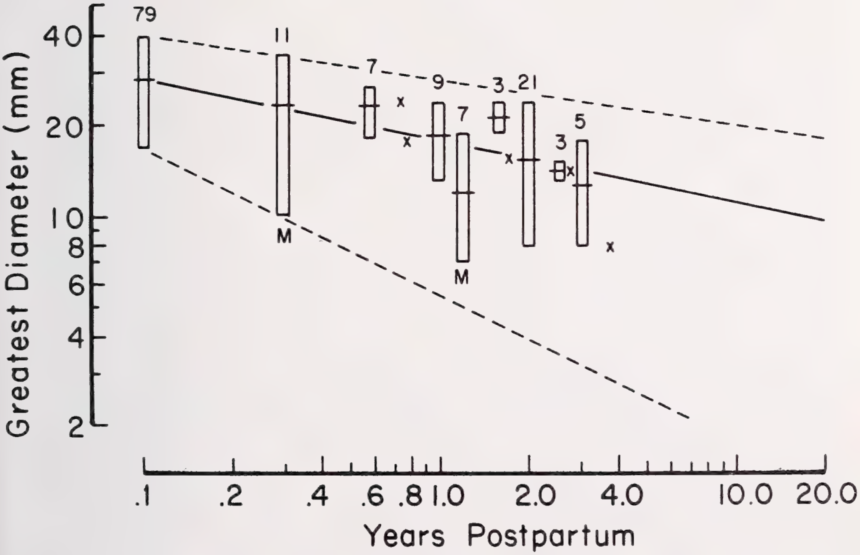


Fig. 123. Postpartum diminution in diameter of the corpus albicans of pregnancy. Bars show range and mean of samples greater than one; sample size is indicated above each bar; x, single specimens. Samples of Atlantic walruses (Mansfield 1958*a*) are distinguished from those of Pacific walruses by M, beneath the bar. Visually fitted curves indicate the estimated mean (solid) and extremes (dashed).

ovulation could be determined with certainty, was shown in Table 27. A *fertile* female is one that is capable of ovulation. Fertility of a given female was diagnosed by the finding in its ovaries of at least one ripe follicle, a corpus luteum, or a corpus albicans. The age at which ovulation first took place, in those with a corpus luteum or corpus albicans, was determined from the size and condition of the corpus and of the placental scar or fetus in the adjacent uterine horn. The resultant data indicate that about 10% of the females were capable of ovulation in their fourth year, two-thirds by the sixth year, and practically all by the eighth or ninth year.

In a sample of 23 females, first ovulations occurred 11 times from the right ovary and 12 times from the left. Second, third, and later ovulations in 52 females occurred 40 times from the right ovary and 37 times from the left. Successive ovulations occurred more often (39 times) from alternate ovaries than from the same one (15 times) ($X^2_{(1)} = 5.6$, $P < 0.02$), indicating that follicular development usually is suppressed for a year or more in the ovary that contained the corpus luteum of pregnancy.

Whereas most pregnancies are spaced at least 2 years apart, Popov (1960*a*), Krylov (1962), and Gol'tsev (1975) indicated that 4 to 5% of 474 females that they examined in late summer were nursing a new calf and were pregnant as well. From those findings they concluded that some animals become pregnant in successive years, but they failed to present convincing evidence of each female's actually having given birth to the calf. Apparently, their conclusion was based only on the presence of the calf and fetus and of milk in the female's mammary glands. As noted earlier, J. J. Burns and I found that 7 of 144 females (4.9%) accompanied by calves in May and June were with foster mothers. One of those foster parents also was newly pregnant. Of the other 137 animals in this series, 1 was newly pregnant and accompanied by its own calf; in that instance (Burns 1965), however, the calf had been born unusually early, and the female apparently had been able to ovulate in her postpartum estrus, before the end of the males' period of fertility. Ordinarily, the postpartum estrus occurs "too late" for fertilization, since it is 3 to 5 months after the fertility period of adult males has ended.

Because the duration of pregnancy in walruses ordinarily is longer than 1 year, the probability that a healthy, fecund individual will ovulate annually and be fertilized appears to be extremely low. The individual's usual interval between ovulations and conceptions should be about 2 years. The work of Krylov (1962), Burns (1965), and Gol'tsev (1975) has confirmed that prediction, as have my findings. In 160 fertile females whose recent reproductive history I was able to trace with certainty, the latest two ovulations had taken place once (0.6%) in the same year, 29 times (18%) 1 year apart, 100 times (62%) 2 years apart, 25 times (16%) 3 years apart, and 5 times (3%) more than 3 years apart. In general, there was a positive correlation between the age of the animal and the length of the interval between the latest two ovulations (Fig. 124).

Since the sample represented in Fig. 124 was drawn from the St. Lawrence Islanders' selective harvest of mainly cows with calves, I assume that it is not representative of the population as a whole but probably is representative of the most productive age classes. That it is biased mainly in the oldest classes is indicated by the fact that half of my specimens over 23 years of age had recently given birth to a calf and showed signs of regular biennial pregnancies, whereas

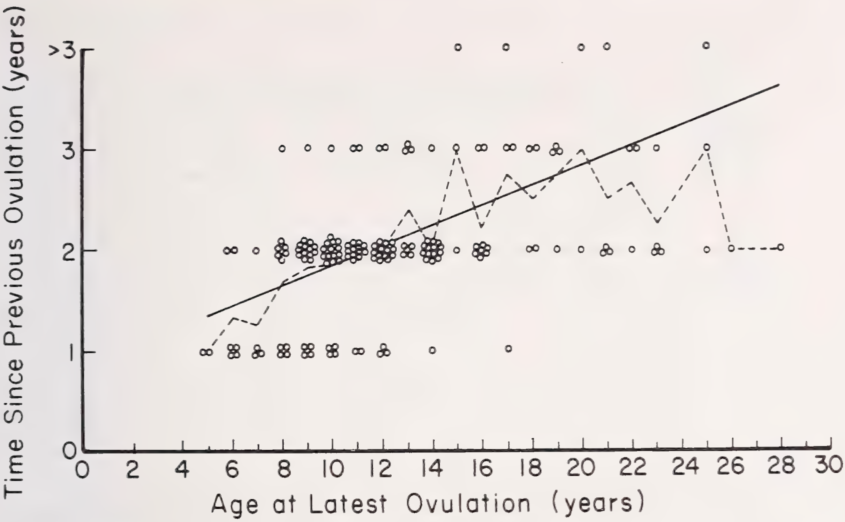


Fig. 124. Time intervals between the two most recent ovulations in Pacific walruses in relation to age. Each point represents one specimen. Dashed line connects the means for each age class at latest ovulation. Solid line is fitted curve (least squares) of means for age classes 6 to 20. (Based on specimens provided by J. W. Brooks, J. J. Burns, K. W. Kenyon, and on the author's data)

Krylov (1966*b*) found no evidence of recent reproductive activity in any of 18 specimens more than 23 years old that were taken nonselectively. The principal effect of selection in my sample probably was deflection of the mean ovulation interval strongly downward in old age, toward 2 years. My findings in the age classes from about 6 to 20 years were comparable to Krylov's (1962) and Gol'tsev's (1975); hence, I assume that these are representative of those age classes. On that basis, I fitted a curve to the data from age classes 6 to 20 by the least-squares method and projected it into the older ages, assuming that this would provide a better estimate of the actual means for those older animals than did the data from the sample.

If the fitted curve (Fig. 124, solid line) value for each age class is taken as the estimated mean interval between ovulations for females in that class, then the reciprocal of that value is the estimated rate of ovulation for females in that class which have ovulated at least once before. For example, the curve indicates a mean ovulation interval for females in their ninth year of life as 1.73 years; hence the probability that a given female which ovulated previously will ovulate again in that year is 58%. Because 99.5% of females at age 9 had ovulated at least once before (Table 27), the number ovulating for the second (or more) time in age class 9 will be 554 per 1,000. The sum of that value and the number ovulating for the first time in that age class (39 per 1,000) is the estimated mean ovulation rate for all females in age class 9 (Table 34).

Although the probability of annual ovulation in walruses would seem to be low because of the long duration of pregnancy, the foregoing data indicate that

Table 34. *Estimation of mean age-specific rate of ovulation for female Pacific walruses of age classes 4 to 30.*

	A	B	C	D	E	
Age class (years)	Est. mean interval between ovulations (years)[a]	Est. mean ovulation rate of previously fertile females[b]	Est. mean fertility rate (per 1,000)[c]	Est. mean no. of females ovulating that ovulated previously (per 1,000)[d]	Est. mean no. females ovulating for first time (per 1,000)[c]	Estimated mean age-specific ovulation rate (per 1,000)[e]
4	–	–	107	0	107	107
5	1.33	0.75	439	80	332	412
6	1.43	0.70	678	307	239	546
7	1.53	0.65	888	441	210	651
8	1.63	0.61	956	542	68	610
9	1.73	0.58	995	554	39	593
10	1.83	0.55	1000	547	5	552
11	1.93	0.52	1000	520	0	520
12	2.03	0.49	1000	490	0	490
13	2.13	0.47	1000	470	0	470
14	2.23	0.45	1000	450	0	450
15	2.33	0.43	1000	430	0	430
16	2.43	0.41	1000	410	0	410
17	2.53	0.39	1000	390	0	390
18	2.63	0.38	1000	380	0	380
19	2.73	0.37	1000	370	0	370
20	2.83	0.35	1000	350	0	350
21	2.93	0.34	1000	340	0	340
22	3.03	0.33	1000	330	0	330
23	3.13	0.32	1000	320	0	320
24	3.23	0.31	1000	310	0	310
25	3.33	0.30	1000	300	0	300
26	3.43	0.29	1000	290	0	290
27	3.53	0.28	1000	280	0	280
28	3.63	0.27	1000	270	0	270
29	3.73	0.27	1000	270	0	270
30	3.83	0.26	1000	260	0	260

[a] From fitted curve, Fig. 124. [b] Reciprocal of A. [c] From Table 27. [d] Product of B age x and C age x – 1. [e] Sum of D + E.

some ovulations occur in successive years. The questions, "How do they occur?" and "Of what significance are they in terms of productivity?" have several possible answers. In my sample, annual ovulations occurred most often where the first shed ovum failed to result in a conceptus (i.e., either was not fertilized or the blastocyst failed to implant), or the fetus was rejected (aborted) early in pregnancy. In each instance, the animal had ovulated again in the following year, but in none had this resulted in two successful pregnancies. Thus, the ability to ovulate in successive years appears to be usually the result of unsuccessful fertilization, implantation, or gestation in the first year.

Burns (1965) reported one instance in which ovulation in successive years apparently resulted in two successful pregnancies. In that instance, the calf of the first pregnancy apparently was born unusually early (probably in February), and the female was impregnated again during her postpartum estrus, probably in April. That this was unusual should be evident from the fact that birth usually takes place from late April to early June, and the postpartum estrus usually occurs in July or August, well after the period of fertility of most adult males. This unusual observation was the only one of its kind among 204 specimens for which Burns and I had obtained sufficient diagnostic data for comparison.

Fecundity

The reproductive efficiency of the female depends not only on the frequency and proper timing of estrus but also on the success in fertilization, implantation, and gestation. The female that achieves each of those steps and successfully produces a calf is considered here as being *fecund.* Hence, *fecundity* is the rate of production of calves.

Several investigators, notably Chapskii (1936), Burns (1965), and Gol'tsev (1975), attempted to assess the fecundity of walruses by counting the numbers of corpora lutea and corpora albicantia in the ovaries, assuming that each of those bodies could be equated with one pregnancy completed. The development of a corpus luteum or corpus albicans, however, is not necessarily indicative of production of a calf. For various reasons, the ovum may not be fertilized, the blastocyst may not implant, or the conceptus may be rejected, resorbed, or born dead (Hafez 1967).

Most earlier investigators did not clearly distinguish in walruses between corpora of pregnancy and those formed from unfertilized or even unruptured (atretic) follicles. Occurrence of reproductive failure was nearly ignored, although Krylov (1966*b*) recognized that all ovulations do not automatically result in pregnancy and success in gestation. Gol'tsev (1975) observed that some pathological conditions in the uterus and ovaries occasionally result in sterility.

In each instance of reproductive failure or success, a corpus albicans will be formed. Retrogression of corpora lutea of pseudopregnancy, as well as of corpora accessoria and corpora atretica also will result in formation of a corpus albicans. Although some of these corpora may tend to be smaller and for that reason less persistently visible than the corpora albicantia from pregnancies, those that do persist cannot be identified with certainty by visual inspection.

For these reasons, the numbers of corpora in the ovaries of walruses are not reliable indices of fecundity, although they should tend to approximate the number of ovulations in an individual's recent reproductive history. Apparently,

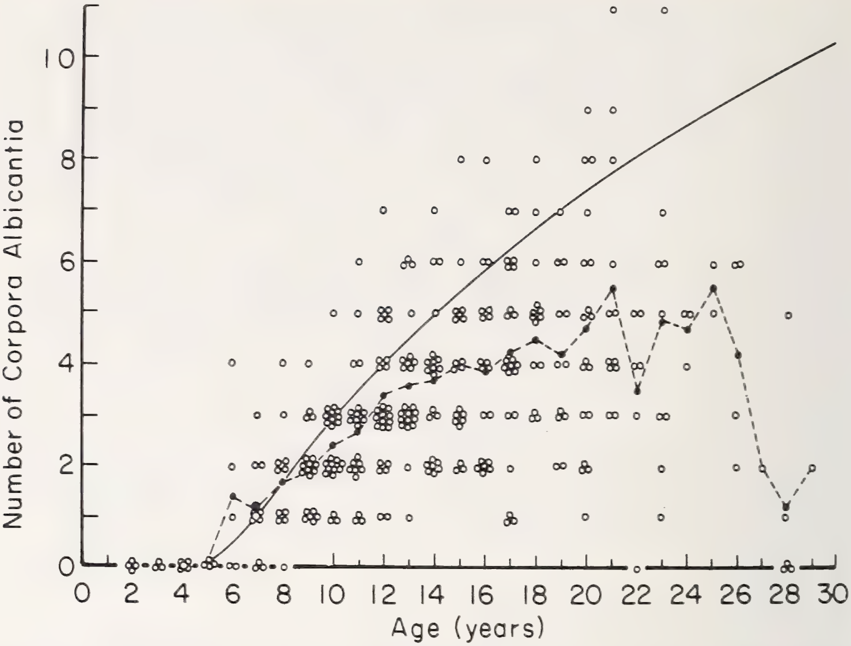


Fig. 125. Comparison of observed with expected numbers of corpora albicantia in Pacific walruses in relation to age. Each circle represents data from one specimen, the age class means of which (dots) are connected by the dashed line. Smoothed curve (solid line) is the predicted age class mean from the age-specific ovulation rate of Table 34, assuming that ovulation at age t_0 results in a corpus albicans at age t_1. (From Krylov 1966*b* and F. H. Fay, unpublished data).

the corpora do not persist indefinitely; some degenerate and disappear after a period of time (Mansfield 1958*a*; Krylov 1966*b*). This is illustrated in Fig. 125, where counts of the corpora in the ovaries of 325 individuals are plotted against the age of the animals. The distribution of data points indicates a tendency for steady increase in the numbers of corpora per individual up to about age 20, followed by a marked decrease thereafter, perhaps to zero by age 30. The steady increase in the early years apparently is the result of long-term retention of most of the corpora; the decline in numbers in old age suggests that all corpora eventually degenerate to the degree that they are no longer distinguishable.

The close correspondence of the empirical mean numbers of corpora per individual per age class (dashed line, Fig. 125) with the estimated means derived from Table 34 (smoothed curve, Fig. 125) suggests that, in most individuals between the ages of 6 and 12 years, all of the corpora albicantia are retained and are distinguishable visually. Thereafter, they seem to disappear at the rate of about one per 2 years up to about age 25, after which they disappear more rapidly.

The only reliable bases for assessing relative success in gestation are the presence of an implanted embryo or fetus in association with a corpus luteum and the presence of a placental scar in association with a corpus albicans. Using those criteria, I ranked my specimens according to their age at the time of their latest ovulation and determined from them their rates of success in conception (implantation) and completed gestations. The results (Table 35) indicate that the lowest rates of success in conception and gestation (40 to 60%) tend to occur in the youngest and the oldest age classes of fertile females; the highest rates (>80%) occur between the ages of 8 and 15 years. The rates of reproductive failure in Pacific walruses appear to be high, relative to other pinnipeds (see review by Harrison 1969), although comparatively lower than in domestic mammals and man (Hafez 1967; Hertig 1967).

Age-related capability for success and failure in reproduction seems to be the rule in mammals (cf. Montagu 1957; Andersen et al. 1962; Belling 1963; Parsons 1964), although most free-living individuals do not survive long enough to reveal a decline in productivity in old age. The walrus appears to be unusual in that respect; some of the oldest females appear to be altogether incapable of reproduction (Krylov 1966*b*).

Because the duration of pregnancy in the walrus is more than 1 year, the individual female tends to ovulate biennially or less often (excluding the postpartum estrus). Hence, less than half of the females in a given year are newly pregnant, and less than half give birth to a calf. On the basis of the sample of 206 potentially estrus females taken in February to August (Table 31), the proportion of such females that are impregnated per year apparently is about 68%; 32% fail to conceive. Of the successful conceptions, about 95% apparently result in completed gestations (Table 35). These findings suggest that, in any given year, about 40% of the females of breeding age will have conceived, 38% will have produced a calf, and 21% will be neither pregnant nor productive. These pregnancy and birth rates are within the range (but somewhat higher than the means) of some derived from another, larger set of data from both Soviet and American sources (see Population). Because all such estimates have been based on samples drawn from a rapidly growing population, they may be typical only of the growth phase. The population at its upper limit, *K*, the carrying capacity of the environment, probably will have a lower birth rate due to later maturation of females and reduced fecundity of adults (Siniff et al. 1978).

Morbidity and Mortality

The walrus has the lowest known reproductive rate for a pinniped, is slow to mature, and has a long life-span. For those reasons, its rate of natural mortality probably is very low. As in most other pinnipeds, however, the causes and amounts of natural mortality in walruses are little known and difficult to determine. Few biologists have had opportunities to examine sick, moribund, or dead walruses in sufficient detail to determine the cause of those conditions. Where natural deaths have been identified, their importance to the population as a whole has been impossible to assess reliably. Although generally acknowledged as a factor to contend with in population dynamics of walruses, natural mortality is so poorly understood that it usually is dismissed as interesting but unimportant, relative to that from the more visible, more accountable harvests

Table 35. *Age-specific rates of success in conception and gestation per ovulation in the Pacific walrus.*

	Conceptions			Gestations			Conceptions resulting in completed gestations (%)
		Successful			Completed		
Year of ovulation	Number ovulating	No.	%	Number ovulating	No.	%	
4–5	6	3	50	6	3	50	100
6	15	13	87	15	13	87	100
7	21	17	81	15	11	73	90
8	21	18	86	18	15	83	96
9	26	25	96	18	17	94	98
10	24	22	92	20	18	90	98
11	27	27	100	23	23	100	100
12	22	21	95	18	17	94	99
13	22	20	91	16	14	88	97
14	19	15	79	19	15	79	100
15	10	9	90	6	5	83	92
16	10	9	90	7	6	86	96
17	6	8	75	5	3	60	80
18	13	10	77	11	8	73	95
19	5	5	100	4	4	100	100
20	6	5	83	4	3	75	90
21–24	10	6	60	9	5	56	93
25–30	9	5	56	9	5	56	100

by man. I regard this poor understanding as one of the major gaps in present knowledge of the walrus.

The following account is a review of the information available from published sources up to 1978 and unpublished data to 1979. It includes information on morbidity and mortality not only from "natural" (nonhuman) causes but from the harvests by man, as well. From a biological aspect, the killing of walruses by man is a form of predation, and it appears to have been the most important single cause of death over the past 120 years or more.

The consequences of this mortality, in terms of its effects on the population, are discussed further in the next chapter. My objective here is principally to document the nature and causes to the extent that they are known. That the information is meager is testimony to the fact that much more work is needed on this subject.

Fetal and Calf Mortality

As considered here, mortality begins *in utero*. Before conception, some of the fertilized ova fail to develop properly and are rejected; some blastocysts fail to implant. My data (Table 35) suggest that preconception failures may be greater than 10% per year; after conception, about 5% of the implanted embryos fail to result in live births.

In the first weeks after birth, some calves die, presumably from neglect, trauma, predation, and infectious diseases. Belopol'skii's (1939), Loughrey's (1959), and my Eskimo informants also expressed belief that some calves die from hypothermia in cold, stormy weather. This seems plausible, for the balance between energy intake and heat loss in these young animals may be easily upset. The surface area of their extremities is relatively large (Iverson and Krog 1973), their metabolic rate is about twice that of terrestrial mammals of comparable size (Iverson and Krog 1973), and their surface temperature (indicative of heat output) tends to be very high (Ray and Fay 1968). The calves appear to require protection by the mother from excessive heat loss, at least during the first few days or weeks after birth, probably until their blubber layer is well developed (Fay and Ray 1968). During very cold or stormy weather, the adults tend to stay in the water which could be thermally disadvantageous for the calf. Unfortunately, there are no reliable indices of death due to hypothermia (Moritz 1953); hence mortality from this cause will be difficult to identify with certainty.

The fate of calves that are abandoned or become separated from the mother by death or accident has not yet been fully determined. Chapskii (1936) and Kenyon (1960*b*) expressed the opinion that all such orphans starve to death, but several investigators have observed that those orphans usually are carried away by another adult when the mother is killed. Burns (1965 and unpublished data), Eley (1978), and I obtained eight unequivocal records in May and June of cows with calves that were not their own, which suggest that fosterage is common. Popov (1960*a*), Krylov (1962), and Gol'tsev (1975) found that 4 to 5% of cows taken in July to September were nursing a calf of the year while pregnant with a new fetus. Because the probability of annual breeding in walruses appears to be very slight, I suspect that those also were calves that had been adopted by foster mothers.

The percentage of calves that survive through the first year is unknown. Probably a few are taken by predators in summer and autumn; apparently a few also die on the autumn hauling grounds from being trampled by adults (see *Intraspecific Traumatization*). There are no records of calves dying during the winter months or of any moribund animals at that time. At 1 year of age, during the northward migration, some youngsters become separated from their parents, and most of these young probably perish. Only a few of them seem to be capable of obtaining their own food, hence of surviving for a time.

Predation

The Pacific walrus is one of the largest and most powerful inhabitants of the Bering and Chukchi seas. As such, it is subject to predation by only a few known or potential enemies: the polar bear (*Ursus maritimus*), the killer whale (*Orcinus orca*), and man.

Polar Bear

The polar bear preys mainly on ringed seals and bearded seals throughout its range (Freuchen 1935; Pedersen 1957; Lønø 1970; Stirling and Archibald 1977), but it is believed to take young walruses occasionally (Parovschikov 1964 *in* Lønø 1970). I know of no confirmed records of predation on walruses. In most instances where bears had eaten walrus flesh, the walruses were known or suspected to have been carrion. Novikov (1962 *in* Nyholm 1975) reported that 22% of the polar bear stomachs that he examined near Franz Josef Land contained parts of walruses. Nansen (1926 *in* Mohr 1952) observed polar bears feeding on the flensed carcass of an adult walrus, and he found another carcass of an adult with skin intact that the bears apparently had inspected but were unable to tear apart. Manning (1961) mentioned that Eskimos found eight bears feeding on the carcass of a walrus at East Bay, Southampton Island, citing this as an example of the bears feeding on carrion. I have seen several dismembered carcasses of adult walruses on the Punuk Islands that had been torn apart and fed on by bears. Lønø (1970) reported that polar bears in the Svalbard area eat walrus carcasses when they are available.

I found parts of the hind flippers of a young walrus in the stomach of a 2- to 3-year-old bear killed near Gambell in January 1957 and pieces of skin and hind flipper from a walrus calf in another from the same locality in May 1966. The Eskimos felt that the bears probably had fed on those walruses as carrion, since several walruses had been shot there not long before the bears were taken.

The best evidence known to me of attempted predation by polar bears on walruses is in three anecdotal accounts by Soviet biologists. Because these are not generally available to English-speaking mammalogists, I quote them here, in translation.

> In August 1935, in Long Strait, we observed a polar bear trying to capture a young walrus. We quote the diary: "At 1:00 pm . . . one of the members of the crew noticed a polar bear approaching a walrus herd which was spread along the edge of the ice for 250 to 300 m. The ice where the walruses were lying was about 80 to 90% occupied. The animals were in groups of from 15 to 20 up to 300 individuals per ice floe, and the total number in the herd amounted to several

> thousands. The herd consisted of adult females with calves, some sexually immature animals of both sexes, and a few adult males. The bear was sneaking up to walruses along the ice. When he was 40 to 50 m from them, he started to run toward them. The frightened animals escaped into the sea, and when the predator reached the ice floe, it was empty. The bear, disappointed, smelled over the spot where he had intended to have his meal, and then slowly continued in the direction of the next group. The bear was rather inclined to approach the groups where there were only females with calves, or else young animals 2 to 3 years old. He approached a herd of adult males cautiously and hesitantly. Conversely, the bulls, feeling their strength, were not frightened by the enemy; they lifted their heads, waiting for him to come nearer. The bear, having approached to 20 m from them, stopped, not daring to move closer. Shaking their heads and showing their powerful tusks, the bulls withdrew into the water. When they were already plunging into the sea, the bear jumped onto the ice floe but, again, with no success. As mentioned previously, the walrus herd stretched along the edge of the ice for several kilometers. While the bear, moving from one end of it to the other, would approach a group of walruses and chase them off into the sea, the next group, still a considerable distance away from him, watched his approach with great attention and then, when he was at a distance of 30 to 40 m, left the ice floe. On one of the floes, the bear managed to catch a young walrus by its hind flippers, at the moment when the latter was about to plunge into the sea. In spite of his great strength, the bear did not succeed in pulling it out of the water; instead, the walrus freed itself and escaped. As a result, the bear chased off the whole settlement without capturing a single walrus" (Nikulin 1941:52–53).

A similar incident, on Peschan Island in the estuary of the Anabar River, northern Yakutia, was reported by Popov (1958:103):

> The walruses on Peschan Island are frequently bothered by bears, which creep up to them under cover of uneven terrain and of driftwood, of which there usually is an abundance along the shore. Sometimes the bears dig pits in the sand or make a pile in front of themselves, in order to hide from the walruses. We saw a bear in a pit dug in the driftwood within 50 m of the herd, where it watched for a long time. Suddenly, it leaped from its concealment and plunged along the flat terrain toward the walruses. The animals, upon seeing the running bear, rushed into the water, and when the bear reached those on shore, only a few large males remained, and these gradually pivoted into the water, threatening with roars and swinging tusks. The bear in his misfortune was unable to decide whether or not to enter the water and only brandished his paws helplessly and growled in discontent. Not infrequently, in the confusion, the adult walruses crush some young; possibly, at the time of the attack, the bears hope to profit from such accidentally crushed or abandoned young.

On Peter's Island (Ostrov Petra), northeastern Taimyr, Popov (1960*b*:97–98) observed a polar bear

> hiding in a sand pit behind a log . . . observing [a group of] walruses from behind and, apparently, was going to attack them. On seeing the people, the bear gave up his hiding place to run directly at the herd. The females with calves and sexually immature animals, which were lying closest to the water, became greatly perturbed and dashed into the sea, where they remained at a distance, not coming out [again] onto the shore. The adult males also abandoned the haulout, but, after the bear left, quickly climbed out onto the shore and lay down in the same place. Some old remains of a young walrus torn up by the bear were located not far from the haulout.

> Near a sand spit at the southern part of Peter's Island, groups and families of walruses amounting to a total of 100 to 120 head were observed on 5 September. The animals stayed in the water and did not haul out on land, on account of the presence on the spit of three polar bears. Apparently, the animals had lain on the shore but were chased into the water by the bears.

In the course of the historic exploration and charting of the Northern Sea Route in 1910 to 1915, Starokadomskii (1976) several times sighted walruses and polar bears together on islands in the Laptev and East Siberian seas in summer. On one such occasion, on the newly discovered Vil'kitskii Island, he found the dried-up skin of a small walrus that apparently had been dragged there and eaten by a bear.

In July 1976, G. C. Ray and co-workers (personal communication) saw several polar bears in association with walruses, along the ice front of the eastern Chukchi Sea. One of the bears was feeding on the remains of a walrus calf, which had been almost completely consumed except for its skin. In June 1978, L. M. Shults (personal communication) sighted a polar bear creeping up on a herd of walruses north of St. Lawrence Island.

These accounts at least confirm that polars bears stalk and chase living walruses, and that they occasionally make contact with them. In other reports, the bears and walruses seemed to disregard each other entirely (Nansen 1926 *in* Mohr 1952; Brooks 1954; Nyholm 1975); in some instances, the bears rather than the walruses seemed to have been the victims (Freuchen 1935:109; Pedersen 1962:51). From all reports and opinions, it is apparent that contact between polar bears and walruses occurs mainly in summer, and that only the younger walruses are really vulnerable to predation. The bears probably are no match for healthy adults in direct combat.

Killer Whale

The killer whale resides in considerable numbers in the Bering and Chukchi seas (Tomilin 1957). Though it seldom is seen in ice-covered areas such as those inhabited by most of the walruses in winter, there is ample opportunity for interaction in spring, summer, and autumn, when the walruses mostly inhabit the edge or the open pack or occur in ice-free waters (Tomilin 1957; Fay 1974).

Belopol'skii (1939) regarded this whale as the walrus' principal natural predator. Scammon (1874:180), Zenkovich (1938*a*), and Nikulin (1941) claimed that its predation is directed mainly at the youngest animals, especially the calves. According to Scammon (1874), the calves, when not otherwise available, are dislodged from the mother's back by ramming her from below. Two eyewitness accounts of killer whales attacking walrus herds in the Gulf of Anadyr were reported by Zenkovich (1938*b*:110):

> The killer whales acted like wolves on land: they surrounded the group of walruses on all sides; then, 6 or 7 on each flank formed straight lines, each whale just behind the head of the next; 5 approached the walruses from the front and 10 came in from behind. Then one of the whales which had come in from the rear burst into the herd and divided it, whereupon the others moved into that location, and the water there boiled as in a cauldron.
>
> In September 1936, I observed a similar systematic slaughter from an SH-2 aircraft, in which I was flying over the Anadyr Gulf in search of whales. About 60 to 70 walruses, headed in the direction of Cape Preobrazhenie, were surrounded

> by a group of about 15 killer whales. We circled a few times over the place at an altitude of 40 to 50 m and were able to follow the tactics of the predators. Exactly as in the first case, the whales closely surrounded the walruses; then, two high fins appeared in the middle of the herd, which separated into groups of 10 to 12 each; the whales "removed" one of those groups in their own way, apparently tearing apart all of the animals. The remaining walruses again united in a compact group and swam toward shore, but the condemned group vanished in a continuous surf.

Zenkovich (1938*b*) found remains of young walruses (as well as bearded seals) in two stomachs from adult killer whales taken in the same locality. The whales, a male and female, were from a group of 20 that were chasing walruses when intercepted by the whalers.

Nikulin (1941:52) observed in Koliuchin Bay that, when killer whales entered the bay, the walruses were disturbed and "threw themselves toward the first ice floe, part of them managing to get onto it, while the others, surrounding the floe, kept close to its edge, trying to remain above the level of the submerged part." He also related the report of a captain of a whaling ship, who observed two killer whales attacking an adult female walrus that was accompanied by three young animals. The young ones "were crawling onto the back of the adult, which kept turning its head toward the *orcae*, threatening them with its tusks." Pedersen (1962) mentioned a walrus that stabbed a killer whale with its tusks. A killer whale that stranded on the northeastern coast of St. Lawrence Island some years ago was reported to have had part of the tusk from an adult female walrus embedded in its side, just behind the right flipper (J. Otiohuk, personal communication). Brooks (1954) reported an incident in which two Eskimos sighted a killer whale and a walrus near Barrow in July and, upon capturing the walrus, found that it was a lactating female. From the actions of the whale and the absence of the walrus' calf, they concluded that the calf probably had been eaten by the whale.

The mortality from attacks by killer whales may have a greater impact on the population than the mere removal of a few calves. Belopol'skii (1939) reported that he had "many times . . . observed carcasses of [adult] walruses killed by this whale" and that, in some of those, "all of the bones were found to be broken." Murie (1936) mentioned the finding by O. W. Geist on St. Lawrence Island of walrus carcasses that seemed to have been "mauled by a killer whale," and I was told by the islanders of several more during the period of my work there. For example, V. K. Slwooko reported to me in 1969 that he had been to his camp on the southern coast of the island early in June and had found there on the beach a carcass of a walrus that apparently had died the same day ("very fresh, no bullet hole"). He stated that it seemed externally to be undamaged, except that the flippers had been severely lacerated ("all torn up"). Internally, he found that all of its ribs had been "smashed." Another animal in the same condition but still alive hauled out near another camp about 16 km away, the same day (J. Aningayou, personal communication).

I examined four walruses that I believe had died as a result of mauling by killer whales. One of these was a calf, no more than a few days old, which was found floating in an area where several killer whales were sighted at the same time. In addition to having lacerations on the hind flippers, this animal had several puncture wounds on its face and several groups of parallel lacerations, 2 to 3 cm

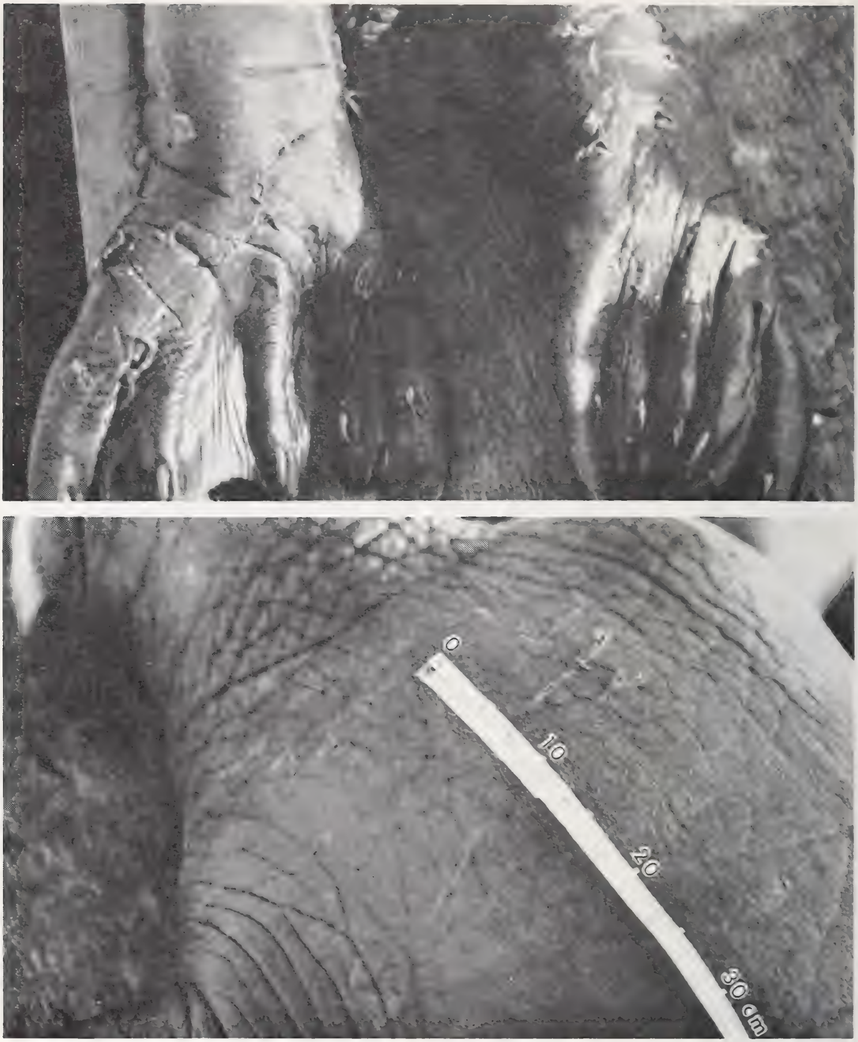


Fig. 126. Lacerations of the skin on the flippers (upper) and shoulders (lower) of a Pacific walrus calf presumed to have been battered by killer whales. (Photos by F. H. Fay)

apart, on the torso (Fig. 126). The lacerations presumably were made by the teeth of the whales. Internally, the walrus showed fractures of most of the ribs, with associated intramuscular hemorrhage. The broken ends of the ribs had punctured both lungs, resulting in release of about 1 L of blood into the thoracic cavity. The liver also had been ruptured, and another 1 L or more of blood had escaped from it into the abdominal cavity.

The second specimen was a subadult male that, apparently, had died at sea and been cast ashore. This animal had an old, infected bullet wound in its shoulder, from which it probably would have died eventually. However, its death apparently had been precipitated by several, more recent injuries. These included (1) extreme laceration of the hind flippers, including fracture of one proximal phalange, (2) secondary contusion of the wounded shoulder, resulting in fracture of the scapula and massive intramuscular hemorrhage, and (3) contusion of the left hind limb and pelvis.

The third specimen, a beach-cast adult female, was intact externally except that its flippers were torn, and it had puncture wounds in the snout and in the rump. These were not bullet wounds, for they had pierced only the skin with no damage to the bones beneath. Internally, however, most of the ribs were broken and there was widespread, deep intramuscular hemorrhage of the thorax. Some of the fractured ribs had punctured the lungs.

The last specimen was a beach-cast adult male, in which the hind flippers were severely lacerated, with some phalanges partly exposed but not broken; it also had numerous punctures and lacerations on the face. Internally, this animal showed massive intramuscular hemorrhage, associated with fractures of both scapulae, all of the ribs, the pelvis, and three sections of the spinal column. The fractured ends of the ribs had punctured the lungs, releasing several liters of blood into the thoracic cavity.

The first and last specimens were in very fresh condition, having died no more than 1 or 2 days before they were found. The second and third had been dead for several months before necropsy but had been well preserved (frozen) in the beach ice. In all cases, the juxtaposition of the hemorrhages and bone fractures indicated that the injuries had been sustained while the animals were still alive, rather than after death. The lack of external wounds (other than superficial lacerations) on the torso adjacent to the internal injuries indicated further that the internal damage had been caused by the animals being struck repeatedly by one or more large, blunt objects with considerable percussive force. Finally, the external lacerations and punctures appeared to have been caused by a series of somewhat pointed teeth of about equal length, with tips 2 to 3 cm apart. The St. Lawrence Islanders claim that such conditions are typical of walruses killed by killer whales, which, according to traditional lore, disable their larger prey by grasping the extremities with their teeth while other whales in the pod ram the victim from below.

The spacing between the parallel lacerations corresponded approximately to the distance between tips of the teeth of immature killer whales (2.5 to 4 cm) and was comparable to the spacing of parallel lacerations on carcasses of gray whales (*Eschrichtius robustus*) known to have been killed by this predator. The internal injuries also seemed consistent not only with the Eskimo lore but with reports by Scheffer and Slipp (1948), Norris and Prescott (1961), and Rice (1968) that use of the blunt snout as a battering ram for killing or disabling other marine animals is part of the repertoire of aggressive behaviors of the killer whale.

Some other, similar instances of mortality in walruses have been attributed to other causes, perhaps incorrectly. Hanna (1920:121) examined five walrus carcasses on St. Matthew Island and two on the Pribilofs and concluded that they "had been crushed by the ice." Later, he examined three more on the Pribilofs and determined that "in each case death had been caused by crushing of the body cavity" (Hanna 1923:213). He surmised that these animals had been killed during the winter, when accidentally caught between ice floes in a storm at the edge of the pack. However, the walrus population in winter does not generally inhabit the edge of the pack, where storm conditions prevail, but resides well north of it where the floes are much larger, more stable, and where there is little or no risk of being crushed.

Murie (1936) reported the finding by O. W. Geist of several walrus bones with healed fractures in archaeological materials from St. Lawrence Island. These included one tibia, one scapula, and two examples of extensive exostosis in the costo-sternal area. Not mentioned by Murie was the fact that his specimens were selected from among thousands of normal skeletal parts (O. W. Geist, personal communication). In a similar series of faunal remains from that island (see Bandi and Bürgi 1972), I found also one pedal proximal phalanx and one tibia with healed fractures. Murie (1936) speculated that the fractures were sustained as a result of killer whale attacks, and this seems to me the most plausible explanation.

Schiller (1954:209) examined 17 of 52 walrus carcasses that washed ashore on St. Lawrence Island in late October 1951 and concluded from reports of intestinal prolapse, the presence of free blood in the abdominal cavity, and his own observations of severe mutilation of the extremities, that they had been killed by a "great and sudden external pressure," possibly "by concussion resulting from an explosion." A series of blasts, heard by the St. Lawrence Islanders in September of that year (and apparently connected with the construction of new port facilities at Providence Bay, Chukotka), were implicated as the possible cause of death. However, in retrospect, the probability of damage by killer whales seems greater, for the following reasons: First, from current knowledge of the distribution and migration of the Pacific walrus, it is predictable that, although a group such as this, made up mainly of adult females and immature animals of both sexes, might have been as far south as the vicinity of southern Chukotka in September–October, the probability of their having been in Providence Bay at that time is extremely remote. Second, internal hemorrhage, coupled with external mutilation of the extremities corresponds most closely (in my experience) to the condition of animals mauled by killer whales. Finally, in his examination of several skulls from these carcasses, Schiller apparently did not notice any of the signs now known to be associated with death of marine mammals from an external, explosive force (i.e., implosion of the rigid-walled air spaces of the nasal passage and middle ear: Rausch 1973). Thus, I feel that the evidence is strongly against death from an "explosive force," and that predation by killer whales is a more plausible alternative.

Harvests by Man

For several millennia before the arrival of European man in the Bering-Chukchi region, the indigenous Eskimo, Chukchi, and other native people preyed on the Pacific walrus population to obtain food and other essential raw materials (Collins 1937; Rudenko 1947; Arutiunov and Sergeev 1968). The numbers of walruses that they killed each year probably did not approach the number of deaths from other, "more natural" causes, for these were essentially Stone Age hunters, who did not have the means or the incentive to take large numbers of walruses. Indeed, they probably relied to a considerable degree on beach-cast carcasses for much of their larder; this is a common practice even now. Conversely, when European man arrived on the scene in the 18th century, he brought with him both the means (large ships, metal weapons, firearms, optical aids) and the incentive (profit) to take quantities far in excess of the requirements for mere survival. The over-exploitation that resulted from introduction of these technological and social innovations was such that walruses were extirpated from some areas in the Bering Sea by the end of the 18th century and severely depleted overall before the last two decades of the 19th century (Fay 1957). Apparently, the retrieved harvests of some 10,000 to 20,000 walruses per year at that time were far greater than the population could sustain. Thus, for a time, man the predator had a significant depleting influence on the Pacific walrus population, and it is probable that his predation continues to be the main cause of walrus mortality.

Until a few years ago, most of the taking of walruses by Alaskan Eskimos in the 20th century was done from homemade boats (*umiak*), which consisted of a wooden frame about 10 m long, 1 m deep, and 1.5 to 2 m wide, over which was stretched a covering of split walrus hides or whole bearded seal hides (see Buckley 1958). In recent years, these boats were powered by an outboard engine, mounted on the stern or in a "well" just forward of the stern. Each boat was manned by a small crew of 3 to 10 people. In some Alaskan localities and along most of the Siberian coast, wooden boats of various kinds were used as well, often with an inboard engine. The umiaks were more versatile than the wooden boats, being more resilient and resistant to the effects of ice. Also, they were light enough to permit them to be drawn long distances over ice by manpower alone. At present, much of the walrus hunting by Alaskan Eskimos is done from lighter weight, aluminum skiffs, manned by two- to three-man crews.

In my experience, weather and ice conditions tend to be suitable for walrus hunting with small boats on about 1 in 3 days during the main spring–summer harvest period; the hunters successfully locate and catch walruses in only about half of those days (Buckley 1958). The animals are killed, generally at a range of 30 m or less, by means of high-powered rifles, mainly of .25 to .35 caliber (6 to 9 mm). Alaskan Eskimos prefer to use full-metal-jacketed bullets for maximum penetration of the dense bones. The preferred target area is the central nervous system when a walrus is lying on ice or land, because the objective is to kill the animal outright, in place. Animals in the water usually are secured by harpoon before the killing shot is fired. Soviet regulations require, and Alaskan hunters prefer, that only those animals lying on the ice be taken, since the probability of their being secured is greatest and the expense in materials is least (Table 36). The kinds of animals taken, in terms of sex and age, vary with the season, location, availability, and local preferences, and, of course, with the current regulations and quotas.

About 80% of the annual Alaskan harvest is taken in May and June in the St. Lawrence Island to Bering Strait area (Burns 1973); 7 to 8% is taken farther north (Point Hope to Barrow) in summer; most of the remainder is taken in the area from Bering Strait to St. Lawrence Island in autumn and winter. Autumn harvests are mainly of animals that have hauled out on shore on the major islands; winter harvests are mainly of animals taken at breathing holes in the ice. Apparently, most of the Soviet harvest by natives is taken during the summer months.

Table 36. *Hunter success in relation to location of walruses.*[a]

Location	No. shot	Animals retrieved		Shots fired per animal retrieved
		No.	Percent	
On ice	62	37	60	5.7
In water	44	20	46	11.1
Total or average	106	57	54	7.5

[a]From observations by F. H. Fay and A. Thayer (unpublished data) at Gambell and Savoonga, St. Lawrence Island.

From the early 1900's to the mid-1950's, the Alaskan retrieved harvest is believed to have ranged from about 1,000 to 1,500 walruses per year (Collins 1940; Brooks 1954; Fay 1957 and unpublished data). These estimates were based on rather fragmentary information, for there was no regular monitoring of the harvests during that time. Soviet retrieved harvests in the first 30 years of this century probably also were about 1,500 per year (Nechiporenko 1927), but this was increased in the 1930's by development of a commercial walrus "fishery" from ships. From 1931 to 1956, the Soviet retrieved harvest ranged from 2,725 to 8,264 (mean, 4,785) walruses per year (Krylov 1968). Apparently, the sexes were about equally represented in Soviet harvests during that time (Freiman 1941); probably more females than males were taken in the Alaskan harvest (Burns 1965). In both, the retrieved harvests were estimated to have made up 50 to 70% of the animals actually killed; the remainder (30 to 50%) was lost due to sinking and wounding (Zenkovich 1938*a*; Buckley 1958; Krylov 1968). Hence, the average annual kill of walruses by man from about 1900 to 1930 probably was about 5,000 animals per year, whereas from 1930 to the mid-1950's, it was doubled to about 10,000 per year. This increase apparently led to depression of the Pacific walrus population. Soviet reports have indicated that, of numerous coastal hauling grounds that were used on the Siberian coast in the early part of the century, only three remained in use by the mid-1950's (Sdobnikov 1956 *in* Kleinenberg 1957; Geller 1957); similar signs of decline were noted in Alaska by Fay (1957).

Perceiving that the population had declined to a dangerously low level, the Soviet Union enacted legislation to end commercial harvests of walruses in the Bering–Chukchi region, beginning in 1957 (Krylov 1968; Kosygin 1975*a*); in the United States this was done 16 years earlier, in 1941 (Brooks 1953; Fay 1957). From 1957 to 1965, the Soviet retrieved harvests declined steadily from about 4,000 to less than 900 per year, and Alaskan harvests fluctuated between 975 and 2,300 per year (Table 37). In both areas, killing of females and calves was greatly restricted during this time, and the sanctity of the principal coastal hauling grounds was affirmed by protective measures. The overall kill (retrieved harvest plus losses) was reduced to less than half of its former level, and the sex ratio of adults in the kill was shifted from about 1 female:1 male to 1 female:3 males. The Alaskan harvests were mainly of adults (Fig. 127). The age composition of the Soviet harvests in that period was very similar (Krylov 1965*a*; Fedoseev and Gol'tsev 1969).

Since 1965, the combined Soviet and American kill (harvest plus losses) of

Table 37. *Retrieved harvests and estimated total kills of Pacific walruses, 1958–77.*[a]

	Retrieved harvests					
	Soviet Union	United States				Estimated total kill[c]
Calendar year	Total	Males[b]	Females[b]	Calves	Total	
1958	4,038	—	—	—	1,500	9,230
1959	3,183	—	—	—	1,400	7,638
1960	2,866	—	—	—	2,300	8,610
1961	2,573	—	—	—	1,860	7,388
1962	1,818	—	—	—	1,690	5,847
1963	1,249	—	—	—	1,725	4,957
1964	1,500	649	255	71	975	4,125
1965	891	1,010	503	254	1,767	4,430
1966	909	1,741	789	278	2,808	6,195
1967	940	1,192	132	23	1,347	3,812
1968	939	933	330	174	1,437	3,960
1969	965	620	186	76	882	3,078
1970	988	881	427	114	1,422	4,017
1971	897	1,592	254	69	1,915	4,687
1972	1,518	847	344	134	1,325	4,738
1973	1,291	1,240	231	110	1,581	4,787
1974	1,205	1,097	263	50	1,410	4,358
1975	1,265	1,488	650	240	2,378	6,072
1976	1,271	1,820	867	302	2,989	7,100
1977	1,461	1,338	650	325	2,450[d]	6,518

[a] Soviet data 1958–64 from Krylov (1968), 1965–77 from unpublished records, Ministry of Fisheries; U.S. data all years from unpublished records, Alaska Department of Fish and Game.

[b] Animals 1 year old and older.

[c] Assuming sum of retrieved harvests = 60% of kill.

[d] Includes 137 adults for which sex was not determined.

walruses in the Bering–Chukchi region has varied between 3,000 and 7,000 animals per year, being lowest in the late 1960's and highest in the mid- to late 1970's (Table 37). The sex ratio in the harvest has continued to be about 1 female:3 males, and the rate of loss of dead and wounded animals apparently has remained stable at about 40% of the overall kill. Both the Alaskan and Soviet harvests have been mainly of adults, principally of the prime, most productive age classes (males 10 to 20 years old; females 8 to 15 years old). However, the continued favoring of females by disproportionate killing of males apparently has tended to offset this removal, for both Soviet and American estimates of the population indicate that it has increased markedly (Kenyon 1972; Gol'tsev 1972; J. A. Estes and V. N. Gol'tsev, unpublished data).

Intraspecific Traumatization

Walruses are very large, powerful animals which frequently engage in agonistic encounters with each other, using their tusks as weapons (Miller 1975*a*).

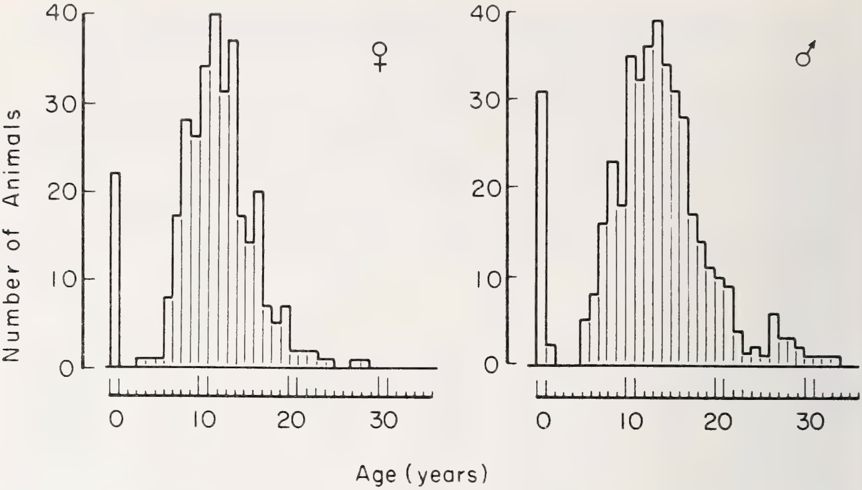


Fig. 127. Examples of age composition of walruses in recent harvests by Alaskan Eskimos: left, males taken at Gambell, Savoonga, and Diomede in spring 1962; right, females taken at Gambell and Diomede in spring 1961. (From Alaska Department of Fish and Game, unpublished data)

Although their thick, tough skin provides some protection from such tusk strikes, severe injuries occur in some instances. Also, because these animals tend to crowd together on the haulouts, there is some traumatization, especially of the young, by trampling (Tomilin and Kibal'chich 1975).

Damages Caused by Tusk Strikes

Walruses characteristically have an abundance of minor scars and lacerations of the skin, especially on the neck and shoulders. Most of these are no more than 1 to 3 cm long and 2 to 5 mm deep, penetrating the epidermis but little more. They are more noticeable on males than on females, possibly because of the sparser pelage on the males; also they are more apparent on adults than on the young, possibly for the same reason. Their distribution on the body seems to correspond in general to that of strikes received from the tusks of opponents (Miller 1975*a*), indicating a simple cause–effect relationship. Walruses of both sexes and all ages strike one another with their tusks, principally while engaging in selection or defense of a resting place on land or ice. The adults, being more powerful than the young, tend to cause more damage.

Large, deep wounds occur commonly in adult males but are uncommon to rare in adult females and younger animals. Such wounds occasionally are punctures that penetrate the skin and blubber but more often are tears into the dermal layer of the skin. These wounds tended to be open and bleeding in males that I sighted in the St. Lawrence wintering area in March but were mostly healing and draining in males that I saw there in April and May (Fig. 128). On the males at Round Island in June and July, most of the wounds already were well healed or at least farther advanced in healing than those seen earlier. For these reasons, I believed that most of the major wounding of adult males takes

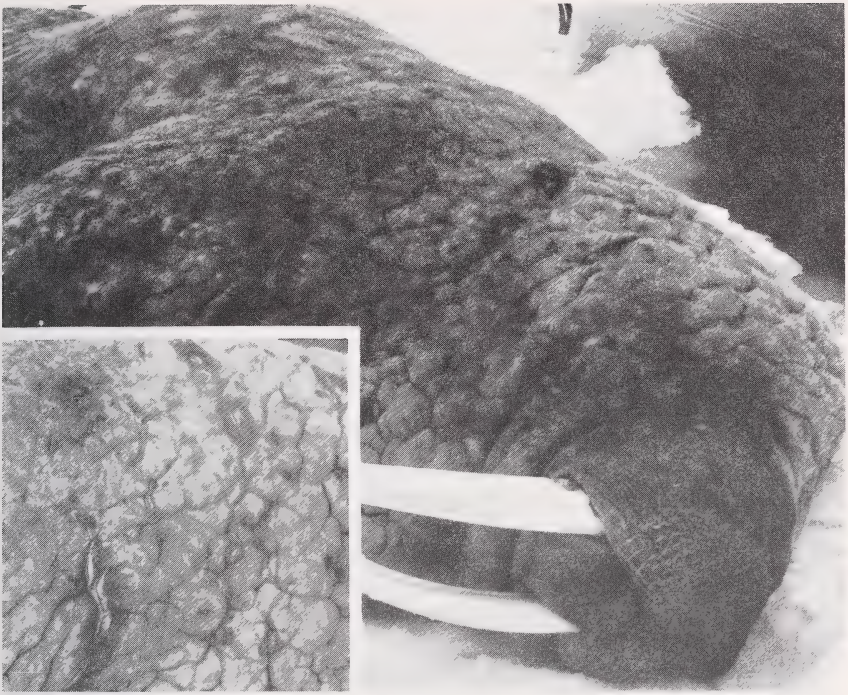


Fig. 128. Healing superficial wounds, presumably from tusk strikes, in the skin on the shoulders of an adult male walrus. The largest wound (lower left, inset) was about 10 cm long. (Photo by G. C. Ray)

place during the mating season, and that the wounds are inflicted by the tusks of opponents, during fights over display "territories." I have observed such fights on only three occasions. In each instance they were the most violent of any interactions that I ever had witnessed. Each took place in the water when the display area of one bull was invaded by another. I did not see any wounding but believe that some took place because of the intensity of these fights. At the time, 6 of 53 (11.3%) adult bulls in the area had open, bleeding wounds; conversely, at Round Island in June and July, less than 1% of the males had bleeding wounds.

K. W. Kenyon (personal communication) reported the following:

> On August 15, 1958 Mr. Alton Y. Roppel found an adult male walrus dead on North Rookery beach, St. George Island, Alaska. The cause of death was not determined. The head was removed and cooked. During cleaning of the skull a tusk tip about 2½ inches long was discovered imbedded in the flesh on the left cheek, under the eye. The skin had healed, so that no external evidence of the imbedded tusk tip was seen prior to dissection.

Apparently, adults are not the only ones damaged by tusk strikes, for I observed a 10-month-old calf that appeared to have been wounded by tusks. Three of its four wounds were deep, bleeding punctures situated along the dorsal midline of the neck and back, about 30 cm apart. The fourth wound, on the rump, did not resemble the others and may have been caused by some other agent. This wound was triangular, about 20 cm on each side, encrusted with dried blood and, apparently, devoid of epidermis and hair. A triangular piece of the outer skin appeared to have been torn off, exposing the dermal layer.

Mortality Due to Trampling

Murie (1936), Collins (1940), Cahalane (1947), and Burns (1965), have cited cases of mass mortality of Pacific walruses, in which many "crushed" carcasses were found high on the beach, well above the high tide line. The crushing was believed to have been due to the animals having either hauled out in panic when pursued by killer whales, or stampeded when frightened by low-flying aircraft. In either event, they were thought to have piled up in the melee, crushing those on the bottom of the pile. Although there is little question about the possible presence of such frightening stimuli, or even about the animals' reactions to them, the matter of some animals' being crushed has been open to question. Gol'tsev (1968) remarked on the finding of numerous carcasses on hauling grounds in the Soviet sector, but did not indicate the cause of death. Tomilin and Kibal'chich (1975) also reported a large number of dead animals, including 21 calves trampled and two fetuses aborted during a stampede from the hauling ground on Cape Blossom, Wrangell Island. The stampede was caused by low-flying aircraft.

All of the reports from the American sector have been from the Punuk Islands, which are situated off the eastern end of St. Lawrence Island (Fig. 1). The animals involved were mostly adult females and young of either sex. According to the St. Lawrence Islanders, this mortality takes place at Punuk in October to December, when large numbers of walruses haul out there during the southward migration. My observations there in January and in March to July, as well as those of several other biologists in March (B. P. Kelly, personal communication), June (L. M. Shults, personal communication), and August (P. E. Tovey, personal communication) have confirmed that living walruses are scarce or absent at Punuk during those months, and that many carcasses are present, none of them fresh. The only sightings of large numbers actually hauled out there and of fresh carcasses have been in October and November (Burns 1965; G. C. Ray, G. Pelowook, personal communication).

My co-workers and I have visited the Punuk Islands five times in June and July (1962, 1975, 1977–1979) and have inspected nearly 700 carcasses there. The carcasses were all comparable in stage of deterioration to those known to have beached on the nearby coast of St. Lawrence Island in autumn. Furthermore, the size and state of dental development of the youngest specimens, the reproductive organs of the adults, and the cementum deposits on the teeth also were consistent with those of specimens killed in October to December. A few of the carcasses were rather flattened, the skin was dry and hard, and much of the hair and epidermis had been lost. The flattened, hairless conditions had been interpreted earlier as being indicative of the animals having been crushed and abraded by the passage of other walruses over them (Murie 1936), but eyewitness accounts from the Eskimos indicated that the advanced decomposition and loss of hair were due more to heating of the carcasses by contact with the living

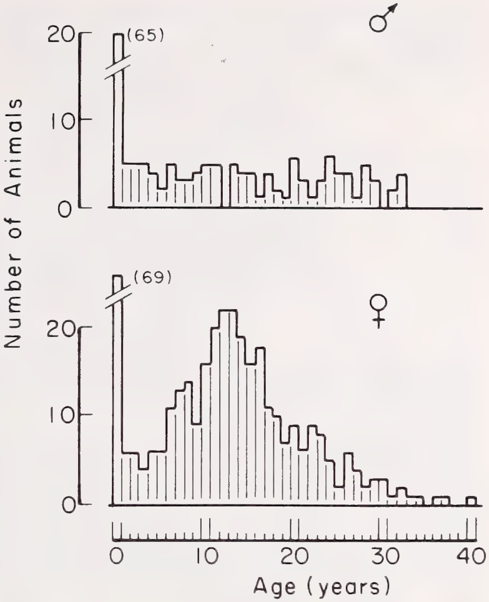


Fig. 129. Age composition of male (upper) and female (lower) walruses that died from intraspecific trauma on the Punuk Islands in 1961, 1974, and 1976–78. (From F. H. Fay, B. P. Kelly, and L. M. Shults, unpublished data)

animals that lay on and around them on the haulout. Because none of the animals had any evident bullet wounds, we judged that all of the deaths were from natural causes. Most of the carcasses were of adult females; only a few of the males were adults (Fig. 129).

We examined by necropsy 29 of the carcasses that had been relatively well preserved by being covered with ice and snow until just before our arrival. Of those, 16 were calves 5 to 6 months old, each of which showed the following primary pathological conditions: extreme contusion and hemorrhage of the cervical musculature, vertebral dislocation, and cerebrospinal hemorrhage (Fig. 130). Several also showed extensive hemorrhagic congestion of the lungs, with extravasation of blood into the thoracic cavity; one showed intestinal prolapse. None was flattened, hairless, or had any premortem bone fractures. None was damaged externally, though most were bleeding from the nostrils. The condition of their lungs and the one case of prolapse suggested the possibility of severe compression; the state of their cervical musculature and spinal cord indicated also extreme torsion of the spine in that region. These conditions strongly suggested that the calves had been rolled and trampled to death by larger animals (i.e., adult walruses).

The conditions in the 13 older animals were remarkably similar to those in the calves. At least nine had died in the same way; two females probably had died from prolapse of the uterus and intestine; one adult male apparently had suffered a fatal concussion from being struck on the head by a blunt object; the cause of death of the 13th animal was not determined. As in the calves, the implication was of their having been rolled and compressed, as might have occurred in a "stampede" situation.

On one occasion (1979), we found numerous aborted fetuses scattered among the larger carcasses. Presumably, these were expelled also as a result of trauma.

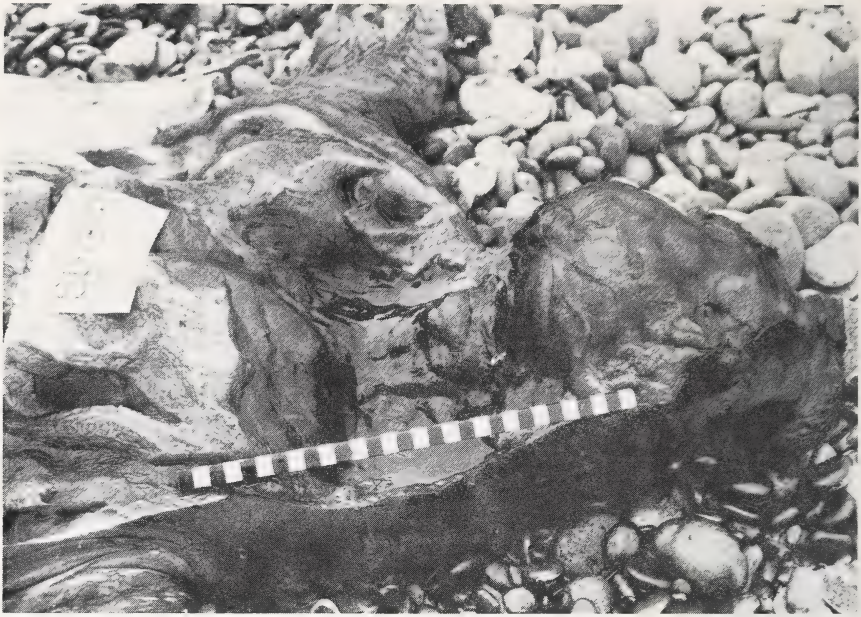


Fig. 130. Intramuscular hemorrhage in the neck and shoulders of a 6-month-old walrus calf that died from intraspecific trauma. Right dorsolateral view with skin, blubber, and superficial musculature removed. Scale in centimeters. (Photo by B. P. Kelly)

Parasitism

Walruses appear to be the least affected of all pinnipeds by parasites (Deliamure 1955; Yurakhno and Treschev 1972). Brooks (1954) and Loughrey (1959) concluded that parasitism does not seem to be an important cause of illness or death in any walrus population at the present time. Sixteen species of parasites have been recorded from the Pacific walrus, and a few of them may be pathogenic.

Ectoparasites

All walruses are infested by the anopluran louse *Antarctophthirus trichechi* (Boheman), which resides in the skin folds over the entire head, body, and appendages, as well as in the external ear canals and about the base of the mystacial vibrissae. This louse is host-specific, occurring only on walruses. Although usually abundant, it does not seem to cause more than mild irritation under natural conditions. Much of the rubbing and scratching that walruses engage in probably is in response to these parasites (Miller 1975*b*). Anopluran lice of related species in other pinnipeds are suspected to be vectors of infection by two genera of filariid nematodes that inhabit the circulating blood as larvae and the right ventricle of the heart as adults (e.g., see Taylor et al. 1961). Neither of those nematodes, however, has been found as yet in any walruses.

A. trichechi occasionally becomes superabundant on walrus calves in captivity, where it is a major source of irritation as well as being unsightly. Treatment with any of several formulations of "Dri-Die 67," a silica aerogel sorptive dust, has been found effective in eradication of the lice (L. R. Penner and W. P. Heuschle, personal communication).

The nasal mite *Orthohalarachne rosmari* (Oudemans) has been recorded once from a walrus that was captured in the vicinity of Franz Josef Land, northern Barents Sea and held in captivity for 7 years in Hagenbeck's Tierpark, Hamburg, Germany (Oudemans 1925). This mite has not been reported again from walruses of either the North Atlantic or North Pacific regions. I searched for nasal mites in the nasal passages and nasopharynx of about 25 walruses from the Bering Sea but found none.

Endoparasites

The internal parasites of the Pacific walrus have been studied most intensively by S. L. Deliamure and his students at the Crimean Pedagogical Institute, Simferopol', USSR. A tabulation of recent findings in walruses from the Chukchi Sea was provided by Yurakhno and Treschev (1972), and by Deliamure and Popov (1975); their findings are reproduced in Table 38.

Trematodes of the genus *Orthosplanchnus* occur frequently in the bile ducts of the liver and rarely in the intestine; I have found them also in the pancreatic ducts. In 2 of 222 walrus livers that I examined, an unusual abundance of these trematodes was associated with fibrous thickening of the bile ducts, to the extent that the liver was visibly and palpably "lumpy." Thickening of the ducts (Fig. 131) presumably takes place in response to irritation caused by the parasites, and this probably has some adverse influence on biliary function.

Cestodes of the genus *Diphyllobothrium*, presumably acquired from ingested fishes, occur infrequently and in small numbers. They localize in the small intestine, where they seem to cause no appreciably irritative or other responses.

The nematodes *Contracaecum osculatum* and *Phocanema decipiens*, also probably acquired from fishes, typically localize in the stomach. In some pinnipeds, they occur there in massive quantities, causing some destruction of the mucosal layer and occasional ulceration of the stomach wall. However, in the Pacific walrus, they are uncommon and, apparently, pathologically inconsequential.

A third nematode, *Trichinella spiralis*, causes severe illness and death in man and some other mammals as a consequence of massive larval invasion of the musculature; its effect on walruses is unknown. Infective larvae of this parasite have been found in skeletal muscles of 2 out of 131 walruses taken in the Bering and Chukchi seas (Rausch et al. 1956; Fay 1960; Yurakhno and Treschev 1972) and in comparable proportions from the North Atlantic region (Fay 1960; Rausch 1970).

Acanthocephalans are the most common internal parasites of the Pacific walrus, usually localizing in the lower (ilial) part of the small intestine and in the colon. The one species identified, *Corynosoma validum*, probably is acquired through ingestion of an invertebrate intermediate host. In my experience, these helminths usually are not very abundant and seem not to cause any significant inflammation or other responses.

Table 38. *Helminthic parasites of the Pacific walrus.*[a]

Species	Location in body	Sample size	No. per walrus (range)	Frequency of occurrence (%)
TREMATODA				
Ohdneriella rossica Skriabin	Liver	?	?	?[b]
Orthosplanchnus arcticus Ohdner	Liver	95	1–7	3.2
Orthosplanchnus fraterculus Ohdner	Liver	95	1–27	8.4
Orthosplanchnus gracilis Treschev and Yurakhno	Liver	95	4	1.05
Orthosplanchnus odobaeni Treschev, Serdiukov, and Yurakhno	Liver	95	1–130	31.6
Orthosplanchnus oculatus Yurakhno	Intestine	95	—	3.2
Microphallus orientalis Yurakhno	Intestine	95	—	14.7
CESTODA				
Diphyllobothrium cordatum (Leuckart)	Intestine	95	1–9	9.5
Diphyllobothrium lanceolatum (Krabbe)	Intestine	53	—	1.7[c]
Diphyllobothrium römeri (Zschokke)	Intestine	95	16	1.05
NEMATODA				
Contracaecum osculatum (Rudolphi)	Stomach	?	?	?[d]
Phocanema decipiens (Krabbe)	Stomach	202	1–25	4.4[e]
Trichinella spiralis Owen	Skeletal muscle	131	—	1.5[f]
ACANTHOCEPHALA				
Corynosoma validum Van Cleave	Intestine	95	1–265	89.5

[a] From Yurakhno and Treschev (1972), except as noted.

[b] Reported only by Skriabin (1915) *in* Deliamure (1955).

[c] Reported only by Deliamure and Popov (1975).

[d] Reported only by Deliamure (1955).

[e] From Yurakhno and Treschev (1972) (N = 95, 1.05%) and L. M. Shults (unpublished data) (N = 107, 7.5%).

[f] From Yurakhno and Treschev (1972) (N = 27, 3.7%), Rausch et al. (1956) (N = 51, 0%), and Fay (1960) (N = 53, 1.9%).

Microbiological Infections

Dermatomycosis

In a sample of 29 animals that I examined, 9 had dermatomycotic lesions on the hind flippers, 1 also had lesions on the fore flippers, and 2 had lesions on the abdomen. This condition appears as dark, ring-like blotches, often with several lesions interconnected (Fig. 132). Histological preparations from one of the abdominal lesions and several of those on the flippers disclosed that the fungal hyphae had invaded only the epidermis, causing partial exfoliation of the cornified layer, occasionally to the depth of the granular layer. Conceivably, in severe cases, this infection might cause intense irritation and exposure of the underlying epidermal layers. It also may predispose the animal to invasion of other infectious agents and irritants. The most extreme case that I observed was of a 10-month-old calf, in which about one-third of the body surface was marked

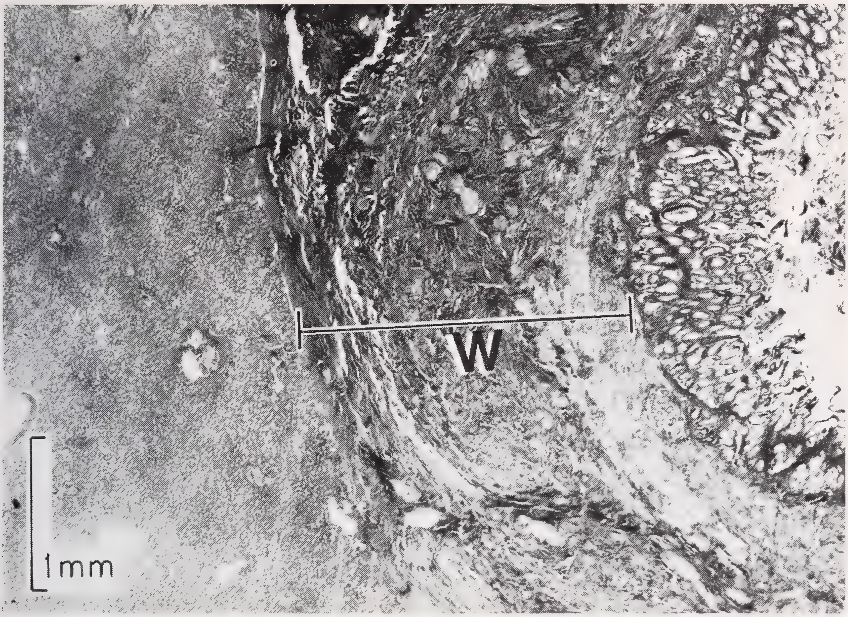


Fig. 131. Photomicrograph of a section through the liver of a walrus, showing fibrous thickening of a bile duct. The wall of the duct (W) is about 2 mm thick, which is about 20 times the normal thickness for a duct of this size. This condition apparently was an inflammatory reaction to presence of the trematode *Orthosplanchnus fraterculus*. (Photo by S. M. Coulthard)

by the ring-like lesions. That animal, nonetheless, appeared to be normally active and healthy in all other respects.

Pulpitis of the Tusks

Bacterial infections of the pulp of the tusks occurs commonly in walruses reared in captivity; I have seen only seven cases in free-living walruses of perhaps 2,000 specimens examined. At least two of these were attributable to bullet wounds (fragments of the bullet were found in the site); three of the others were certainly identified as having been caused by other traumatic agents, possibly tusk strikes by other walruses. In six cases, purulent exudate was draining to the exterior through one or more perforations of the maxilla near the proximal end of the tusk; in three cases there was extensive periodontitis, as well. The principal effect of such infections seems to be shedding of the affected tusk, which may have grave social consequences but probably is of little importance otherwise. The possibility of spread of the infection to other organs, for example, by inhalation of the purulent exudate, may have more lethal consequences. In an adult male and an adult female with abscessed tusks, the principal drainage from the abscess was through a hole in the wall of the left nasal passage, whereby direct inhalation of the exudate would have been unavoidable. I examined only the head of the male but was able to perform a complete necropsy of the female,

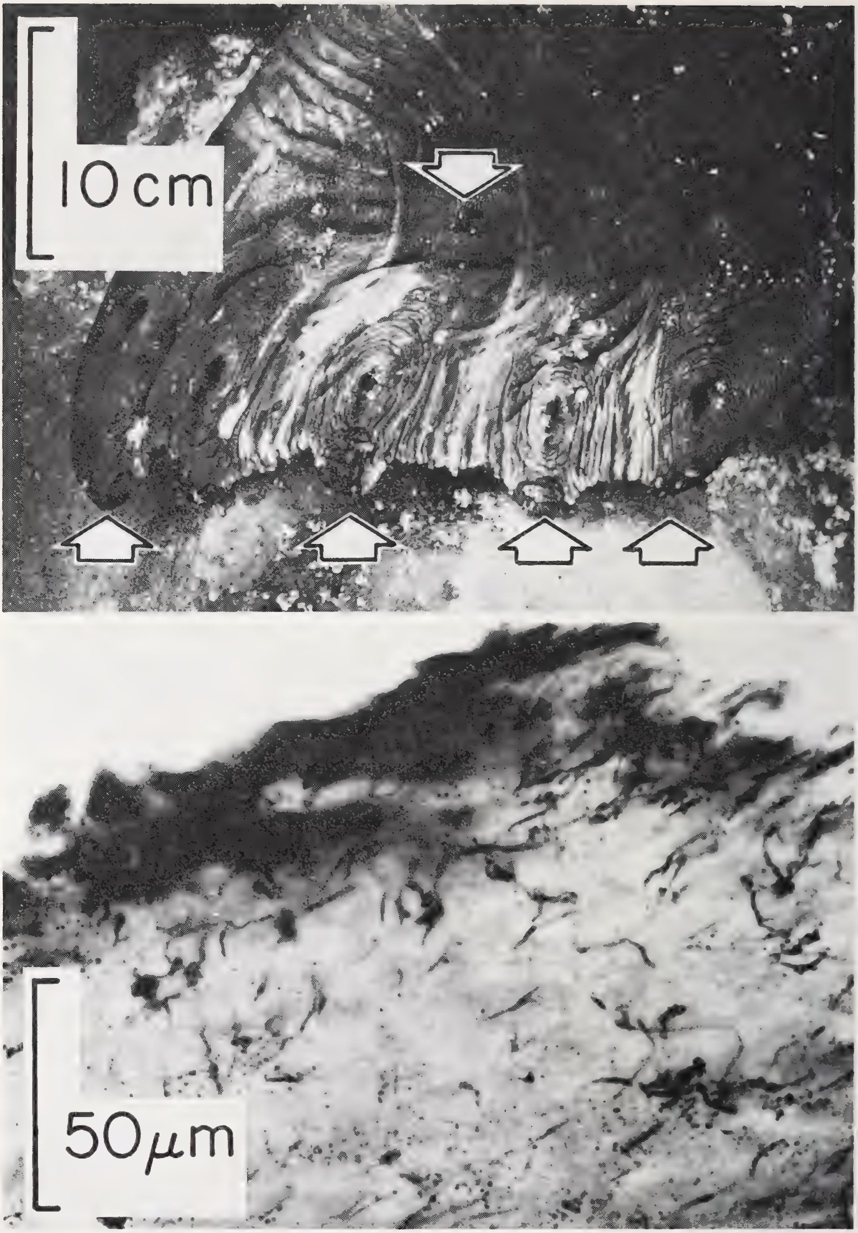


Fig. 132. Mycotic lesions on the foreflipper of a Pacific walrus (upper). In this instance, the major lesions were on the tips of the digits (arrows); another small lesion can be seen on the dorsal surface. The presence of mycelia and spores of the fungal agent was demonstrated in the stratum corneum of one of the lesions (lower) treated with Gomori's stain. (Photos by F. H. Fay)

which was cast ashore dead on the southern coast of St. Lawrence Island. The entire respiratory tree of that female had been affected, leading to hepatization (solidification) of most of the lungs. In addition, there was severe pleural and pericardial inflammation with associated adhesions of the organs to the body wall, fibrous thickening of the pericardial sac, and production of 7 to 8 L of milky fluid in the thoracic cavity. The animal seems certainly to have died as a consequence of those conditions.

Conjunctivitis

Apart from occasional damage to the eyes caused by tusk strikes, abnormal ocular conditions seem to be uncommon in walruses. I observed only one case of apparent conjunctivitis, in which one eye was swollen and nearly cemented shut by a large amount of yellowish-green exudate. The animal, an old male, was extremely emaciated and lethargic and had several open, bleeding wounds on its body. Since this was in late March, at the end of the mating season, the leanness and wounds probably were not related to the eye infection but to fights with other bulls for display sites.

Urethritis

A 3-year-old male taken at Gambell on 1 June 1957 was affected by a generalized inflammation of the entire urogenital system, probably as a result of a bacterial infection of long standing. The urethra was greatly inflamed, thickened, and enlarged, and the testes and epididymides were swollen. The penis also was inflamed and showed extensive osteonecrosis of the baculum. The bladder contained a large amount of milky fluid. Conceivably, the kidneys also had been affected, but they had been discarded before I was able to examine them. The animal as a whole was emaciated, apparently having been severely debilitated for some weeks or months.

Pleuritis

Two adults, a male and a female, showed generalized nodular fibrosis of the visceral and parietal pleurae, indicative of chronic inflammation. About 3 L of clear, serous fluid also were present in the thoracic cavity of the male; a lesser amount was present in the female. Apart from those conditions, both animals appeared to be normally healthy in all other respects. Probably, "the inflammatory process began as the result of pneumonia or pneumonitis" (J. G. Bridgens, personal communication).

Pneumonia–Pneumonitis

Minor inflammations of the respiratory tract seem to occur commonly in walruses, for it is not unusual to see yellowish to greenish mucous expelled from the nares (suggestive of catarrhal inflammation of the nasal membranes) or to hear animals wheezing during respiration (suggestive of bronchial congestion). A. C. Heinrich (personal communication), who spent several years as a school teacher on Little Diomede Island, reported to me that "extremely thin animals with large portions of the lungs decayed or atrophied . . . are sometimes found."

Calves may be particularly susceptible to respiratory conditions. Five of 17 calves that were captured alive near Gambell in May showed signs of nasal congestion (frequent expulsion of yellowish to greenish mucous from the nares); another developed such a condition after four days of confinement in an outdoor pen. One of these calves, with unusually foul-smelling breath and watery stools at the time of capture, died within 24 h with acute, nonspecific congestive pneumonia. Three of the calves apparently were cured by intra-muscular injections of wide-spectrum antibiotics; the fifth calf apparently overcame the condition spontaneously, after about 3 days confinement in an artificially heated room.

Subdermal Bullae

Eskimos at Barrow in 1970 killed an adult female that had virtually no blubber. In the hypodermal layer, however, were numerous fluid-filled cysts up to 1.5 cm in diameter (Fig. 133). A piece of the skin with the cysts in place was forwarded to R. L. Rausch, who determined histologically that these cysts (bullae) were epidermal invaginations. Presumably, they were inflammatory responses to a microbiological agent.

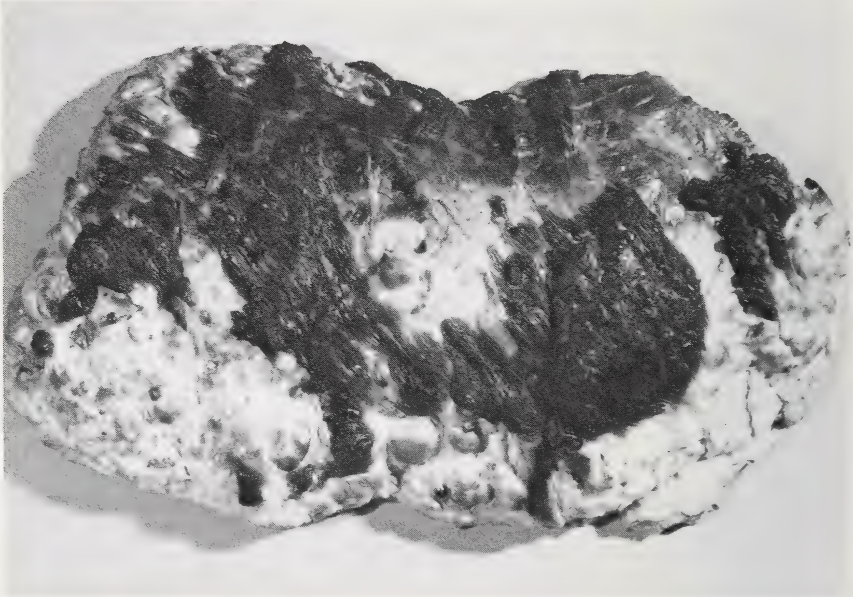


Fig. 133. Subdermal bullae in the blubber of an adult female walrus taken at Barrow, Alaska. View of inner surface of the blubber with some superficial muscles (dark areas) in place. Rounded nodules in the blubber are fluid-filled cysts lined with a single layer of epithelial cells, apparently derived from the epidermis. Scale in centimeters. (Photo by G. C. Kelley)

Leptospirosis and San Miguel Sea Lion Virus

Serum samples from 55 walruses taken in the Pribilof wintering area during

March–April 1976 were screened against *Leptospira pomona* monovalent antigen in slide agglutination tests. All results were negative. Fifty-four of the same serum samples were tested for antibodies to San Miguel Sea Lion Virus infection, also with negative results (A. W. Smith and D. G. Ritter, personal communication).

Miscellaneous Nonspecific Conditions

Aneurysm

An adult female, taken in outer Bristol Bay had a large, sterile cyst (20 cm in diameter) on the ventral surface of the spleen (Fig. 134). The cyst was turgid, filled with a mixture of fresh and necrotic blood, and its walls were about 3 mm thick. The histological character of this cyst indicated that it was an aneurysm, a localized dilatation of one of the splenic arteries, probably of long standing (R. A. Dieterich, personal communication). An aneurysm of this size could be expected to cause some pain through pressure and, perhaps some erosion of adjacent organs.

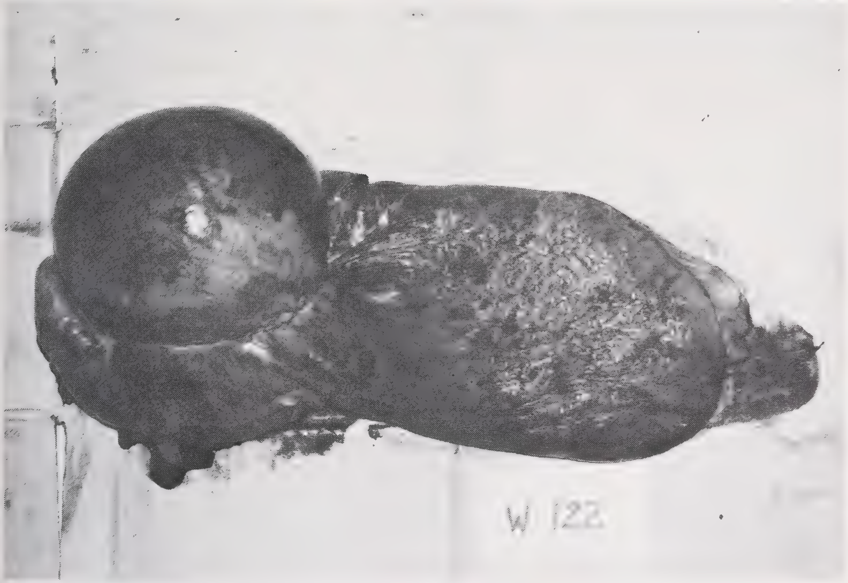


Fig. 134. Arterial aneurism (left) in the spleen of an adult female Pacific walrus. The cyst, about 20 cm in diameter, was filled with blood. Card at lower right is 127 × 76 mm. (Photo by F. H. Fay)

Uterine Tumors

Brooks (1954) mentioned the finding of intra-uterine "cysts of unknown nature" that "appeared capable of occluding the lumen of the affected horns" in 2 of about 40 uteri examined by him at Little Diomede Island in the spring of

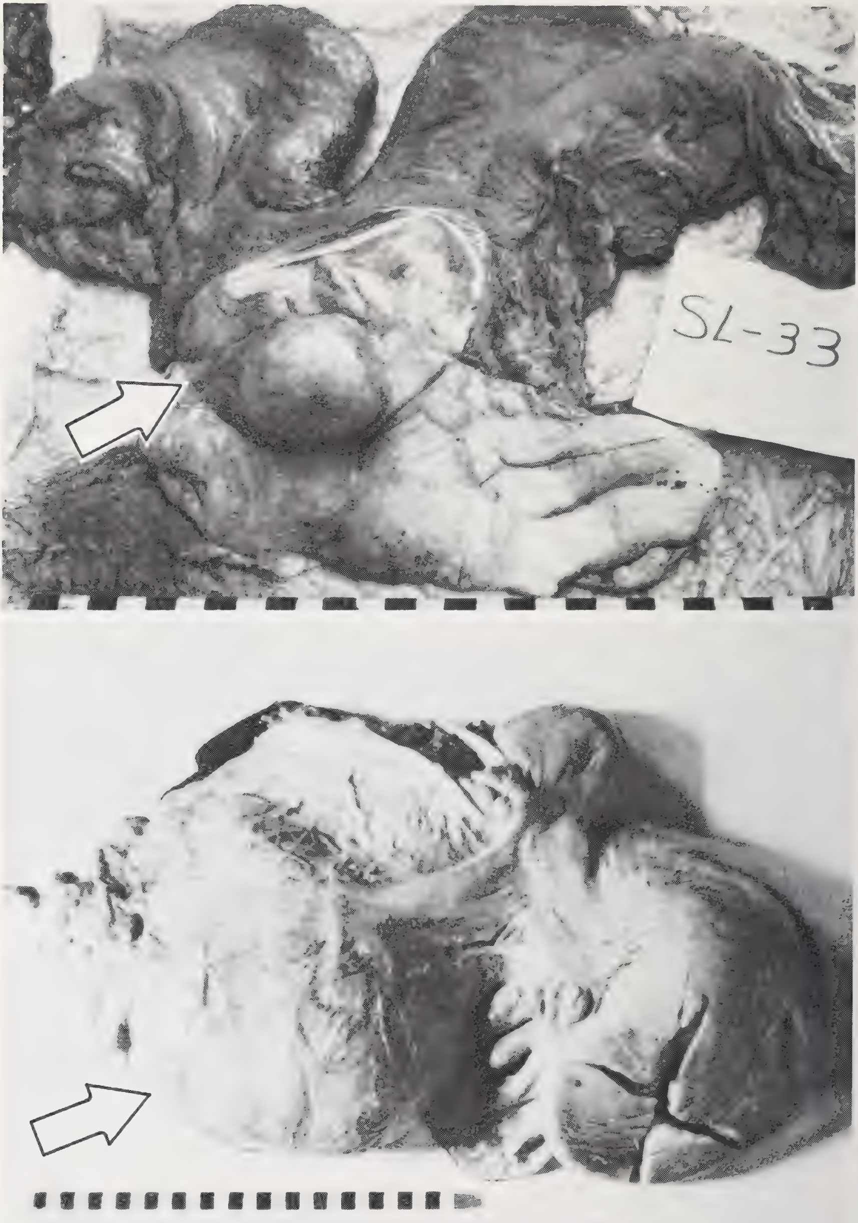


Fig. 135. Tumors of the cervix in some Pacific walruses: upper, posteroventral view (uterine horns at top, bladder at lower right) with cervix opened by ventral incision to expose a small spherical tumor (arrow) in its wall; lower, dorsal view (uterine horns at right) showing the greatly enlarged cervix, in the wall of which was a large tumor (arrow). Scales are in centimeters. (Photos by F. H. Fay)

1953. A. C. Heinrich (personal communication) reported a "tumor of the womb" in another animal taken in the same locality. Tumors of the cervix seem to be relatively common in Pacific walruses, for I have seen at least four in 240 uteri from animals 2 years old and older. The largest of these, about 15 × 20 cm, had fully occluded the left uterine horn, which contained about 2 L of purulent fluid (Fig. 135). The right horn of this specimen, however, remained fully functional, as indicated by the presence of a recent (2- to 3-week-old) placental scar and associated large corpus albicans in the ovary.

Cystic Ovaries

Cystic ovaries occur infrequently. I have seen three cases, drawn from a sample of more than a thousand adult females examined by Burns (1965 and unpublished data) and me. In each case, the cysts apparently were of long standing, since they were filled with caseous, necrotic material. In two cases, only one ovary was affected; in the third, both ovaries were totally affected, and the animal consequently was sterile.

Umbilical Hernia

A beached carcass of an adult female, found on the southern shore of Bristol Bay by R. A. Dieterich and L. M. Shults (personal communication) had a herniated umbilicus, through which had emerged part of the uterus and of the fetus therein (Fig. 136). The adult appeared otherwise to have been in excellent condition. Presumably, the herniation had been caused by trauma.

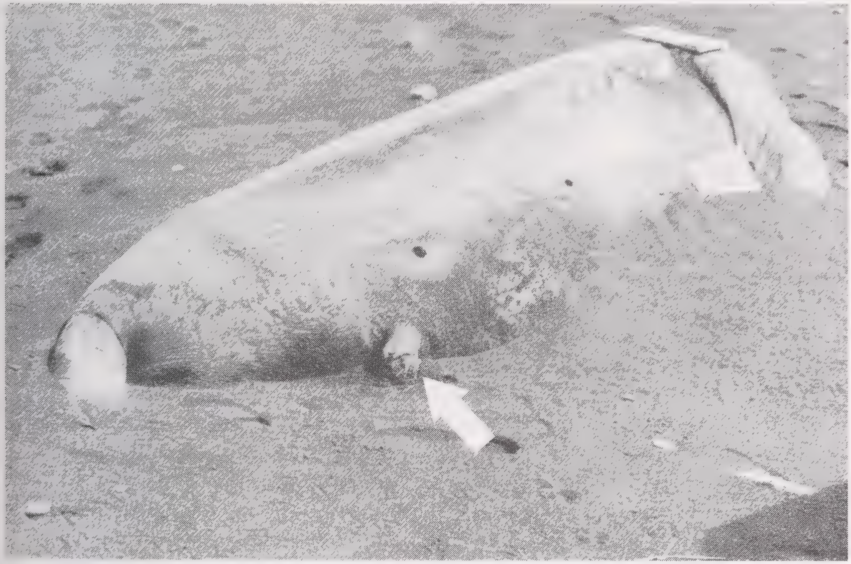


Fig. 136. Umbilical hernia in an adult female walrus. Extrusion of part of the uterus and hind limbs of the full-term fetus (arrow) through the ruptured abdominal wall apparently had caused the death of this animal, shown here in posteroventral view. The two holes in the right abdominal wall were made by scavengers at the mammae. The base of the right hind limb is visible at left. (Photo by R. A. Dieterich)

Renal Calculi

One kidney of an adult female taken at Gambell contained two large (6 mm), irregular, tan-colored calculi (stones) in its pelvis. Analysis of one of the stones by infra-red scanner (Reference Laboratory, Newbury Park, California) disclosed that it was composed principally of carbonate-apatite (90%) and calcium oxalate monohydrate (10%) (R. A. Dieterich, personal communication).

Congenital Deformity

A case of anomalous tridactyly of the forelimbs in a calf taken at Savoonga, St. Lawrence Island, was reported by Marks and Burns (1966). An X-ray plate of the right forelimb showed underdevelopment of metacarpals, carpals, and phalanges, as well as unusual attenuation and folding of the soft tissues. The left limb appeared more normal, except that it had only three digits. The authors speculated that such deformity would have led to early death of the animal, which was extremely thin and weak.

Frostbite

In the far northern localities where walruses occur in winter, animals sleeping on the ice occasionally may lose access to the sea when the lead through which they had emerged is closed by movement of the ice or perhaps by rapid refreezing. Individuals presumed to have been beset by such circumstances have been seen to progress over ice and land, apparently in search of open water (Freuchen 1935; Murie 1936; Perfil'ev 1970). Freuchen and Salomonsen (1958:53) remarked that, "these wandering walruses certainly have a difficult time. We have encountered cows which had a little cub along—both of them frostbitten on the front of the flippers and the mother without a quarter inch of blubber." Frostbite probably does not occur otherwise, for it ordinarily would be prevented by re-entering or remaining in the water.

Entrapment in Heavy Ice

The Eskimos of Savoonga often have reported to me that individuals and small herds frequently become entrapped in areas of stable, heavy ice north of St. Lawrence Island in winter. They stated that the animals generally maintained one or two breathing holes but appeared to be greatly restricted in their feeding range because they were obliged to remain in the vicinity of those holes for long periods—sometimes several weeks or months. Some of those animals became extremely emaciated, presumably because they had exhausted the food supply within range of the holes. Conceivably, some entrapped animals may die from starvation under such conditions.

Physical Exhaustion

Physical exhaustion may be a common debilitating factor during the autumn migration, for the animals swimming southward in the open sea, ahead of the advancing ice, often are disadvantaged by severe southerly storms with heavy seas. Often, they must swim hundreds of kilometers against the seas before making a landfall, whereupon they come ashore in droves, usually on traditional hauling grounds (Gol'tsev 1968, 1972). At St. Lawrence and the Punuk Islands in autumn, the animals that come ashore during or following severe storms are said by the Eskimos to be extremely lethargic and to strongly resist being driven back into the sea. From this, the islanders have concluded that the walruses are physically exhausted from their long swim and require rest before continuing on their way. In addition to being vulnerable to terrestrial predators (especially man), animals in that condition may be predisposed also to contraction of infectious diseases and to traumatization by other walruses.

Damage by Rockslides

Several of the hauling grounds used by walruses in the Bering–Chukchi region are on beaches beneath high, rocky cliffs. Occasional landslides and falling rocks from the cliffs apparently maim and kill a few animals. One example of this kind of mortality was identified by B. P. Kelly and R. M. O'Connor (personal communication) on Round Island in 1979. In that instance, an adult male with crushed skull was found beneath a rockfall; a necropsy of the specimen revealed no other plausible cause of death. Other examples have been recorded in the same locality by J. Taggart and C. Zabel (personal communication) in previous years.

Overview

The frequency of occurrence of pathological conditions and their effects on walruses individually and as a population are not yet well documented. The evidence at hand indicates, at least, that the causative factors are numerous and that few of them are age- or sex-specific in their effects. For most of the past 120 years, the main mortality of walruses in the Bering–Chukchi region appears to have been caused by man's harvests of these animals, for the population was severely depressed at least twice during periods when harvest levels were unusually high (see Population). An increasing body of evidence points as well to a large, comparatively unnoticed natural mortality, which has been and still is more difficult to evaluate.

Presumably, the natural agents of morbidity and mortality described in the foregoing account are the very ones that exerted a regulating influence on the primitive population, before intensive harvesting began. Yet another agent, malnutrition, may have been the proximate regulator, for the food supply is finite and its replacement rate is comparatively low. The synergistic effects of malnutrition with most of the natural agents mentioned here could cause profoundly increased mortality. Malnutrition also probably depressed reproduction.

The overall rate of mortality from all causes was estimated by Burns (1965) as being about 13% per year, based on the age composition of samples from the harvest. Fedoseev and Gol'tsev (1969) believed that the basis for Burns' estimate was unreliable and that the indicated rate was erroneously high. Harvest samples generally are not representative of age composition, because of hunter selection and the tendency for sex- and age-segregation in a nonrandomly distributed population. Fedoseev and Gol'tsev (1969) speculated that actual mortality was no greater than 8 to 10%, based on the maximum age of animals in the population (about 40 years). Obviously, there is little agreement and no firm evidence at present on which to base estimates of mortality, which probably differ widely between years and between the different sex and age classes.

Population

The world population of walruses in 1978 probably included more than 200,000 animals, about 80% of which were in the North Pacific (Bering–Chukchi) region. The actual numbers are unknown but certainly were in that order of magnitude. Clearly, these animals were much less numerous than they had been a few centuries earlier. In all parts of their distributional range they were severely depleted by commercial exploitation at various times during the past 350 years. Although protected to some degree in all areas in recent years, the North Atlantic populations still have not recovered. Only the North Pacific population appears to be approaching its pre-exploitation level.

The history and current status of walrus populations in the North Atlantic region and in the Laptev Sea were reviewed by Reeves (1978). In this chapter, my principal objective is to summarize briefly the known history and vital statistics of the North Pacific population.

Identity

The walrus appears to be a relative newcomer to the North Pacific region, for the fossil evidence of its presence there dates back no more than about 100,000 years to the middle Pleistocene (Sangamon) interglacial stage (Hopkins 1967; Repenning and Tedford 1977). At that time, climate and sea temperatures in Beringia apparently were somewhat milder than at present, and sea ice in winter extended no farther southward than the vicinity of Bering Strait (Hopkins 1972). I presume that walruses first entered the area at that time from the northwest, having traversed the northern coast of Eurasia from the North Atlantic region.

At present, walruses are essentially circumpolar in distribution (Scheffer 1958), but they are not uniformly distributed. There are several areas of concentration, between which few or no walruses have been sighted in recent times (Fig. 3). This discontinuity suggests the presence of several discrete populations which have little or no chance of interbreeding. The present isolation of some of those populations probably resulted from depression of their numbers by overharvests. Differences in body and tusk size between some regional concentrations, however, even as close as Hudson Bay and Foxe Basin (Mansfield 1958*a*), suggest longer reproductive isolation.

Walruses of the Bering–Chukchi region differ from those of the Laptev Sea principally in size (Heptner et al. 1976), and these two populations are physically separated by at least 1,200 km of unoccupied or sparsely occupied sea. Individuals and small groups occasionally stray from the Chukchi Sea as far west as the mouth of the Kolyma River and Bear Islands (Chapskii 1940; Nikulin 1941), but strays from the Laptev population have been sighted no closer than the eastern part of the New Siberian Islands, some 350 km away (Chapskii 1940; Popov 1960*b*). Hence, there appears to be little if any possibility of extensive interchange between the Laptev and Pacific populations.

Pacific walruses differ from those in the eastern Canadian Arctic not only in size but in other morphological characters, such as shape of snout and shape of mandible, which presumably are genetically controlled (Allen 1880; Mansfield 1958*a*; Pedersen 1962; F. H. Fay, unpublished data). The main concentrations of these two populations are separated by at least 1,600 km. Although strays from the Chukchi Sea occasionally reach the southeastern part of the Beaufort Sea and Coronation Gulf, and those from the Canadian population occasionally reach northern Banks Island (Harington 1966), there is little probability of significant interchange between these two populations.

The Pacific walrus population at present appears to be both physically and reproductively isolated from all others. Its closer craniological resemblance to the Laptev than to the Canadian walruses, in my opinion, suggests that its most recent connections have been to the west, rather than to the east.

History

In an earlier report (Fay 1957), I briefly outlined the history of the Pacific walrus population from the beginning of its commercial exploitation in the 18th century to the middle of the present century. A more complete review of the historical record is in preparation, but for the present, a brief synopsis will suffice.

Before the arrival of European man in the Bering Sea, the Pacific walrus population must have comprised at least 200,000 animals, for it could not have withstood the commercial harvests that followed had it been any smaller (Fay 1957). Its actual size, however, is unknown.

More than 10,000 walruses were reported to have been harvested commercially in some years during the late 18th to late 19th centuries (Sumner 1868; Elliott 1886; Clark 1887; Petrof 1900; Arsen'ev 1927). The main products from those harvests were ivory, oil, and hides. In the beginning, most of the animals taken were from all-male herds summering in the southern part of the Bering Sea, especially in Bristol Bay and on the Pribilof Islands. In a 2-year period, some 18 tons of walrus tusks (4,000–5,000 animals) were obtained on the Pribilofs alone (Tikhmenev 1863). The Pribilof herds were nearly extirpated by the beginning of the 19th century (True 1899), and the exploiters turned their attention northward, into the pack ice zone. This change probably resulted in larger numbers of females being taken thereafter, because the females tend to stay with the ice.

In the second half of the 19th century, the harvesting methods also changed from the use of harpoon and lance (by which means nearly all of the animals killed were retrieved) to shooting with rifles (by which many of those killed or wounded were not retrieved; Clark 1887). I believe that this change (about 1866) had a significant effect on the walrus population, for not only were larger numbers taken and retrieved, but at least as many more were killed or wounded that could not be retrieved. Nye (1879 *in* Allen 1880:768) and Petrof (1900) estimated that the numbers of animals retrieved in the late 1800's amounted to no more than one-fourth to one-third of the numbers killed. Because ivory was the prime objective of those harvests, calves and other very young animals were not taken. Hence, many dependent young were deprived of parental care.

According to Clark (1887), the calves were set free with the expectation that they would be fostered by other females. I suspect that many of those calves did not survive.

The increased mortality brought about by these practices apparently resulted in a drastic decline of the Pacific walrus population in the late 19th century (Allen 1880, 1895; Clark 1887), and this ebb was perpetuated in some degree by continued commercial harvests in the beginning of the 20th century (Dobbs 1911; Chandler 1943; Madsen and Douglas 1957). That the population was at a very low level in the early 1900's was recognized in both North America and Eurasia (Dobbs 1911; Arsen'ev 1927; Chandler 1943; Fay 1957; Krylov 1968). According to Madsen and Douglas (1957), the United States government in 1909 prohibited commercial harvesting of walruses within Alaskan territorial waters. This prohibition did not apply to the taking of walruses on the high seas or in Soviet waters, however, which continued at least until 1913. At that time, the prices for ivory and hides steeply declined on the American market, making it no longer profitable to hunt walruses commercially (Madsen and Douglas 1957).

Some commercial hunting by Americans resumed after World War I (Nechiporenko 1927; Arsen'ev 1927; Chandler 1943). This hunting apparently was much less intensive than before, partly due to scarcity of walruses, discouragement by Soviet patrols, and further regulation. The killing of walruses in Alaska, except for local use by natives, was prohibited by U.S. Department of Commerce regulation in 1937 and by the Congressional "Walrus Act" of 1941 (Ch. 368, 55 Stat. 632, 48 U.S.C. 248). Ten years earlier, however, the Soviet government had begun an intensive commercial harvesting program from vessels (Zenkovich 1938*a*). Those harvests from 1931 to 1957 apparently precipitated the second major decline of the Pacific walrus population (Geller 1957; Kleinenberg 1957; Fay 1957; Kosygin 1975*a*). It is from that low ebb that the population is recovering at present.

Rigid regulation of harvests by both the Alaska Department of Fish and Game and the Soviet Ministry of Fisheries, beginning in the late 1950's, limited the numbers taken and were especially restrictive of the taking of females and young. The harvests before that time probably had included more females than males (Burns 1965); this was changed by the new regulations to about 75% bulls, 20% cows, and 5% immature animals. That change probably had a considerable effect on the composition of the population itself, tending to enhance its productivity by increasing the proportion of females in the population.

At the same time, both the Soviet Union and the State of Alaska provided protection to herds using the major hauling grounds on shore. Walrus hunting was forbidden on and near eight hauling grounds in the Soviet Far East (V. Mineev, personal communication) and on one (Round Island) in Alaska. Thus, the impact of human predation on the Pacific walrus population was considerably lessened during the 1960's and 1970's.

Enumeration

Marine mammal populations in general are difficult to census directly because they tend to be "patchy" in distribution, unequally visible (some being under water), and distributed over enormous areas that are difficult or impossible to survey in an acceptably short period of time (Chapman et al. 1977). The walrus is no exception, and indirect methods for estimating population size, such as mark–recapture and interpretation of catch statistics, have not been developed sufficiently to supplant direct counts.

Mark–Recapture

Some efforts have been made to develop methods for marking walruses but principally for the sake of tracing their migrations, rather than estimating population size. Mansfield (1958*a*) marked 115 animals in the Canadian Arctic with a metal disk-tag having a harpoon-like point that penetrated the skin. Krylov (1965*b*) used a similar tag to mark 500 walruses in the Bering and Chukchi seas. Brooks (1954) marked 11 calves in Bering Strait with a metal strap-tag attached to the hind flipper, and J. W. Brooks, K. W. Kenyon, and I (unpublished data) applied 12 more of those tags to males at Round Island in 1958. None of the Canadian, Soviet, or American tags has been recovered, probably because too few animals were marked. The metal tags also may have caused inflammation of the tissues and damage from freezing, both of which could result in sloughing of the tag, not long after application. The technical difficulties in marking a large enough proportion of the population for estimation of its size by the mark–recapture method appear insurmountable at present, but the possibility of marking large numbers on the coastal hauling grounds in autumn should be explored. Some lesser amount of marking would be appropriate also for tracing migrational patterns, as noted earlier, and this probably can be accomplished in the near future by satellite tracking.

Catch Statistics

Interpretation of walrus catch statistics appears to have little value for estimating actual population size, although it may be useful as an indicator of minimum size and of major changes in status. Fay (1957) estimated that the population before 1860 must have contained at least 200,000 animals, based on the reported size of the late 19th century harvests and on assumptions as to the composition and gross productivity of the population. That the walrus population declined drastically by 1880 as a result of those harvests was widely recognized. Marked decline was indicated also by the poor hunting success and consequent mass mortality of Eskimos at St. Lawrence Island in the winter of 1878–79 (Rosse 1883; Allen 1895; Petrof 1900). Until then, the islanders' annual catch of walruses had been sufficient to support about 1,500 people, about half to two-thirds of whom died in the famine that winter (Muir 1917). The scarcity of walruses there at that time apparently was partly due to adverse ice and weather conditions which excluded the animals from some areas and prevented the hunters from ranging far from home (J. Otiohuk, personal communication). Had the walrus population been larger, however, adequate numbers of animals probably would have been available, for that kind of reliability would have been a prerequisite for the founding of the walrus hunting culture on St. Lawrence Island more than 2,000 years earlier.

The irregular and occasionally insufficient numbers of walruses taken at St. Lawrence Island in the 1940's to 1960's (Table 39) also suggested that the walrus population at that time was smaller than was required for reliable subsistence

Table 39. *Numbers of walruses retrieved by St. Lawrence Island Eskimos in 1940–68. (During this period each village required at least 120 to 125 animals for human and sledge dog food and other uses.)*[a]

	Village	
Year	Gambell	Savoonga[b]
1940	315	?
1946	170	?
1947	180	?
1948	70[c]	?
1949	250	?
1950	300	?
1952	275	?
1953	200	175
1954	70[c]	120
1955	125	30[c]
1956	150	330
1957	200	270
1958	150	300
1960	280	425
1961	300	250
1962	435	510
1963	275	240
1964	120	240
1965	445	390
1966	490	510
1967	85[c]	300
1968	465	115[c]

[a] Data from Hughes (1960), J. W. Brooks and F. H. Fay (unpublished data), and unpublished records of Alaska Department of Fish and Game. Years in which harvests were not recorded are omitted.

[b] Question mark indicates quantity unknown.

[c] Insufficient harvests.

harvests (Fay 1957 and unpublished data). Again, ice conditions had a major influence on the numbers available to each village. The smallest harvests at Gambell in 1940–68 were taken in years of very light ice cover in the Bering Sea and very early breakup and dispersion of ice between St. Lawrence Island and the Chukchi Peninsula. In those years, the walruses apparently wintered much farther north than usual and had mostly vacated the Gambell area by the time of the traditional spring hunt. Conversely, the light ice cover allowed the Savoonga hunters to have early access to the walruses, and to take an adequate harvest. The smallest harvests at Savoonga were taken in years when the ice remained compacted against the northern side of the island until late June, preventing the hunters from launching their boats before most of the animals had left that area. In those years, the ice was more favorable at Gambell, and adequate harvests were taken there. The largest harvests in both villages were mainly the result of availability of walruses during unusually favorable ice conditions in autumn. In those years, large supplementary harvests were taken during the southward migration of the walrus population.

Although ice apparently played a major part in determining the availability of the animals to the St. Lawrence Islanders in 1940–68, adequate harvests probably would have been taken in all years, had the walrus population been larger. In that period, the Eskimos of the island numbered only about 550 to 600 people — about one-third as many as in the early 19th century. Nonetheless, even with modern firearms and other advantageous equipment, they were unable to obtain enough walruses in some years to meet their minimum requirements. If remedial food supplies had not been provided by Federal and State governments, the islanders probably would have been afflicted again by starvation and death, at least in 1954–55, as they were in 1878–79. For those and other reasons (Fay 1957; Geller 1957), I believe that the Pacific walrus population was at a lower level in the 1940's and 1950's than it had been at any time within the past 300 years.

Aerial Census

The best estimates of the size of the Pacific walrus population have been derived from sample counts during aerial surveys by Soviet and American biologists (Table 40). In each instance the total size of the population was estimated by extrapolation from the numbers counted in sampled areas to the total area of occupation. The first such survey was conducted in the western Chukchi and eastern East Siberian seas in August–September 1958 by P. G. Nikulin (*in* Fedoseev 1962), who counted about 20,000 animals on the coastal hauling grounds and estimated that at least 20,000 more were at sea. A more intensive survey by Fedoseev (1962) of the same area and of the northern Gulf of Anadyr in September–October 1960 yielded an estimate of 46,000 animals in Soviet waters; at least 4,000 more were assumed to have been in waters off Alaska. Earlier, Kenyon (1960*a*) and co-workers conducted two aerial surveys of the population in its wintering area in the Bering Sea from February to April 1960 and derived estimates from each of about 70,000 to 100,000 animals. A similar estimate was obtained from a third survey in March 1961 by K. W. Kenyon (unpublished data). In September–October 1964, Gol'tsev (1968) estimated 47,000 to 71,000 walruses, mainly on the coastal hauling grounds of Chukotka, and in April 1968, K. W. Kenyon (unpublished data) obtained an estimate of 73,000 to 110,000 from a fourth aerial survey over the Bering Sea pack ice. From aerial surveys in Soviet waters in September–October 1970, Gol'tsev (1972) counted 62,000 animals on the hauling grounds and estimated the total population at 101,000. A fifth survey by Kenyon (1972) of the population in the Bering Sea pack ice in April 1972 yielded a conservative estimate of 85,000 to 162,000 walruses. Finally, a Soviet–American cooperative survey in September–October 1975 in the Chukchi and western Bering Sea gave an estimate of 140,000 to 200,000 animals (Estes and Gilbert 1978; J. A. Estes and V. N. Gol'tsev, unpublished data).

None of these estimates should be regarded as actual counts. Each is unreliable to some degree because of problems encountered in obtaining and interpreting the data on which it was based. Ray and Wartzok (1976), Chapman et al. (1977), and Estes and Gilbert (1978) have reviewed most of those problems in detail.

The Soviet estimates, in each instance, were lower than those from the

Table 40. *Size of the Pacific walrus population, estimated from aerial surveys between 1958 and 1975.*

	Estimated population (thousands)		
Date	Range	Median	Source
August–September 1958	–	40	P. G. Nikulin (*in* Fedoseev 1962)
February–March 1960	78–113	95	Kenyon (1960*a*)
April 1960	70–100	85	Kenyon (1960*a*)
September–October 1960	–	50	Fedoseev (1962)
March 1961	70–100	85	K. W. Kenyon (unpublished data)
September–October 1964	47–71	59	Gol'tsev (1968)
April 1968	73–110	92	K. W. Kenyon (unpublished data)
September–October 1970	–	101	Gol'tsev (1972)
April 1972	85–162	123	Kenyon (1972)
September–October 1975	140–200	170	J. A. Estes and V. N. Gol'tsev (unpublished data)

American surveys conducted about the same time. The reasons for this are not yet clear but seem to be related to procedural differences. Whereas the American estimates were based on extrapolation from counts along randomly placed strip transects, the Soviet estimates were based on photographic counts of animals on the hauling grounds plus conservative guesses as to the numbers at sea (not sampled). Extrapolation from the American strip transects to the total area occupied could have led to overestimates or underestimates, due to the nonrandom distribution of the animals (Estes and Gilbert 1978). The Soviet counts only of animals on the haulouts probably were low, due to underestimation of the proportion of the population at sea. In both the Soviet and the American surveys, the population estimates were based mainly on animals that were sighted out of the water, on land or ice, for there was no known method to account for those under water and not visible to the observers. This probably contributed substantially to underestimation in all instances.

Because walruses are large and their coloration contrasts well with the background, especially when they are lying on the ice, they are easily sighted from low-flying aircraft. Walruses seem to spend much more time out of the water in all seasons than do most other pinnipeds (Fay and Ray 1968), but they are more widely distributed than is optimal for short-term aerial surveys, and their patchy distribution can lead to large errors in extrapolation to areas not covered by the surveys. Their tendency to congregate requires aerial photography for optimal counts of large herds. Insufficient knowledge of their activity rhythm has made estimation of numbers not sighted (in the water) difficult at best and generally untenable.

Whereas the Soviet and American estimates shown in Table 40 were derived by different methods and gave different results, each set suggests a trend of rapid increase of the population over the past 20 years. Some of that trend could have been due to improvement in survey methods, greater knowledge of distribution, and increased effort. The more recent surveys have been more extensive than earlier ones, and have made greater use of aerial photography and more sophisticated statistical methods than in the earlier surveys. Nonetheless, the probability that the population has increased is high, because of the great reduction in magnitude of the harvests. Furthermore, increase has been indicated also by recent reoccupation of abandoned hauling grounds (Gol'tsev 1968; J. J. Burns, F. H. Fay, V. N. Gol'tsev, unpublished data), as well as by expansion of range to pre-exploitation limits (Kosygin and Sobolevskii 1971; Pinigin and Prianishnikov 1975).

The quality of future surveys probably could be improved by sampling most intensively in the areas of greatest concentration of animals. The distributional data now available suggest that the optimal times for such sampling would be in February–March (Figs. 5,6) or in August–September (Figs. 11, 12). In those months, distribution of the animals appears to be most concentrated, most predictable, and most stable. The major areas to be covered in February–March would be the St. Lawrence concentration and the Bristol Bay (including Pribilof) concentration. Each of those probably could be surveyed separately since there seems to be little possibility of interchange between them in those months. Although each concentration covers about 200,000 km², the animals are likely to be most concentrated in about one-fourth to one-half of that area. With modern high-speed aircraft and capabilities for infrared radiometric sensing (IRS), preliminary visual or IRS mapping of distribution could aid greatly in designing the survey for maximally effective coverage (see Ray and Wartzok 1974).

The concentrations in August–September occupy a much larger area than those in February–March: about 300,000 km² in western and southern Chukchi Sea (Soviet waters), at least 150,000 km² in the eastern Chukchi Sea (Alaskan waters), plus several thousand square kilometers in the vicinity of the major hauling grounds in Bering Strait, the Gulf of Anadyr, and Bristol Bay. Hence, the problem of obtaining adequate samples would be greater, and the feasibility of conducting a preliminary visual or IRS reconnaissance would be practically excluded. Also, because the behavior of animals using coastal hauling grounds probably differs from that of animals in the pack ice, the results might require different interpretive methods for each area. Because of restrictive regulations applying to Soviet and American air space, the actual survey would need to be done cooperatively with very close coordination and communication between nations.

Insofar as possible, the preliminary reconnaissance and the surveys should be conducted within the first 24 h of fair weather following a storm, because the animals probably haul out more often under those than under other conditions (Nikulin 1947; J. Taggart, personal communication). Surveys during very cold or very windy weather should be avoided, for walruses generally stay in the water when the surface "windchill" (Siple and Passel 1945) is equivalent to still air temperatures of −25°C or less (Fig. 137). Animals in the water are more difficult to sight than those on the ice at distances greater than 0.5 km from the flight path of the aircraft (Kenyon 1972; Estes and Gilbert 1978; F. H. Fay, unpublished data). Hence, the in-water sightings will be reliable only within a narrow band along the flight path. Animals on ice generally are easily seen and counted within 1 km of the aircraft. On the basis of surface:subsurface times given in Table 26 and as summarized by Ray and Watkins (1975), the number of animals sighted in the water probably tends to be about one-fourth to one-ninth

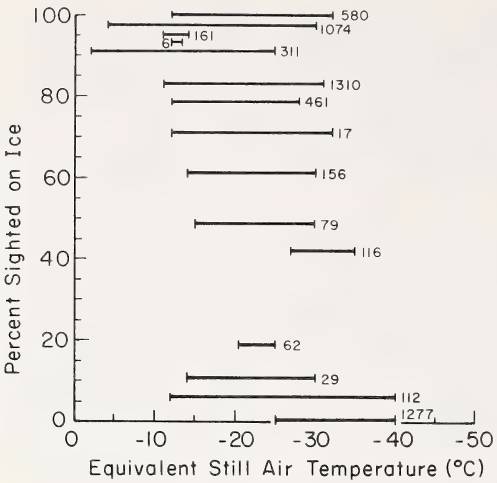


Fig. 137. Percentage of walruses sighted on the ice (versus in the water), in relation to the range of equivalent still-air temperatures. Equivalent temperatures based on measured air temperatures and surface wind velocities ("windchill": Siple and Passel 1945) at the time of sighting from icebreaking ships in the Bering Sea in February to April. (From J. J. Burns, J. A. Estes, F. H. Fay, and G. C. Ray, unpublished data)

(mean, one-sixth) of the actual number present in the water.

Aerial photographic capability seems essential, to minimize human error in visually estimating the numbers of animals in large herds. Accurate counts of groups larger than 10 to 15 animals usually are not feasible from the moving aircraft; small animals are particularly difficult to detect in large groups, even in aerial photos. Walrus groups on ice tend to be larger than those in the water and largest on the coastal hauling grounds (Fay and Ray 1968; Estes and Gilbert 1978). Furthermore, they differ seasonally and regionally in size (Table 41) as well as in composition. Males tend to be in smaller groups in winter and early spring than in late spring and summer (Table 42); females tend to form larger herds than males in all seasons and to congregate most in late spring and summer (the "nursery herds" of Burns 1970).

Composition

The sex–age composition of the Pacific walrus population was estimated earlier by Freiman (1941), Fedoseev (1962), Burns (1965), Krylov (1968), and Fedoseev and Gol'tsev (1969), each of whom concluded that immature animals of both sexes made up about 30 to 40% and that the sexually mature adults made up about 60 to 70% of the population. The sex ratio at all ages was assumed to be about 1 male:1 female, based on the known ratio at birth. Each of those estimates was based in part also on samples of animals observed at sea, on samples from the catch, and on analogy with other mammalian populations. Each was admittedly imprecise but was remarkably similar to the others, considering that each was based on a different set of field and harvest data. Although this similarity suggests that each estimate was close to the actual composition, the investigators acknowledged that sampling error, especially in the catch data, could have been large because of selection for certain size classes. Also, by analogy with other polygynous pinnipeds, a 1:1 sex ratio of adults seems highly improbable.

Table 41. *Percentage frequency of occurrence of group sizes of Pacific walruses on ice and in water, in relation to time and location.*[a]

			Group size							
Location	Date	No. of groups	1	2	3–4	5–9	10 – 15	16–35	36–96	>96
On ice										
Eastern Chukchi Sea	Sept. 1978	118	8	6	12	6	16	29	16	8
St. Lawrence concentration	April 1972	340	17	14	11	11	11	15	12	8
Bristol Bay concentration	April 1968	364	18	18	14	16	12	9	6	5
St. Lawrence concentration	March 1972	112	48	16	9	6	6	7	5	2
In water										
St. Lawrence concentration	April 1968	103	38	23	16	11	3	7	2	0
St. Lawrence concentration	March 1972	233	51	19	13	7	3	2	3	2
Bristol Bay–Pribilof conc.	March 1976	116	52	28	15	3	1	1	0	0

[a] Sources: Estes and Gilbert (1978), Kenyon (1972 and unpublished data), and F. H. Fay (unpublished data).

Table 42. *Percentages of animals in groups of different sizes in relation to time.*

Group type and time	No. of animals	Group size 1	2	3–4	5–9	10–15	16–35	36–96	>96
All-male									
February–April	428	18	14	24	21	6	17	0	0
May–June	382	4	1	1	8	3	5	0	78
Females and young									
February–April	1,940	1	7	6	9	9	28	24	16
May–June	1,054	1	6	2	4	3	8	19	57

I have attempted to reconstruct the Pacific walrus population about the years 1960 and 1972, drawing on data from several sources.

Population in 1960

In September–October 1960, during an aerial census of the walrus population in the western Chukchi and Bering seas, Fedoseev (1962) noted that herds of adult males were easily identified by their pale, pinkish color, in contrast to the darker, browner coloration of herds made up mainly of adult females and young of both sexes. On that basis, he determined that the number of individuals in all-male herds made up 32% of the animals in Soviet waters. In the same area, in August–September 1961, Krylov (1968: Table 4) determined from shipboard counts of some 30,000 individuals that the animals in all-male herds made up about 42% of the total. This proportion is different from that provided by Fedoseev, but the imprecision inherent in both samples is such that they are acceptably similar as "rough estimates." Krylov's counts indicated that 43.5% of animals in all-male herds in Soviet waters were in the Bering Sea (Gulf of Anadyr), and 56.5% were in the western Chukchi Sea.

In September 1960, Krylov (1966*a*) estimated visually that 8 to 10% of the males using the Rudder Spit hauling ground in the Gulf of Anadyr were immature individuals "not more than 3 years old." His criterion of "tusks reaching 20 cm," however, indicates that they actually were up to 5 years old (cf. (Fig. 81). Gol'tsev (1968) determined the age of 348 males harvested on Rudder Spit between 1937 and 1956 and found that 14% were up to 5 years old, 43% were 6 to 9 years, 27% were 10 to 14 years old, and 16% were more than 14 years old. He suspected that the sample was biased by selection of young animals, but he apparently was unable to confirm that. Hence, this is the best estimate available of the age composition of the Rudder Spit herd, and of males summering in the western Bering Sea, at that time.

The all-male herds in the Chukchi Sea, according to Krylov (1966*a*), were composed of 40% immature animals under 6 years old in 1960. Conversely, the age composition of males harvested in that area in 1960 to 1964, as depicted by Fedoseev and Gol'tsev (1969), indicated 1 to 8% under 6 years, 4 to 16% 6 to 9 years old, 23 to 48% 10 to 14 years old, and 34 to 61% 15 years and older. The compositions of these harvests presumably were biased by selective taking of the largest animals, but they suggest at least that the all-male herds in the Chukchi

Table 47. *Pregnancy and birth rates in the Pacific walrus population indicated by the composition of harvest samples.*

				Fertile females[b]					
			Sample	Barren		Pregnant		Bearing	
Sample[a]	Locality	Date	size	No.	(%)	No.	(%)	No.	(%)
A	Chukchi Sea	July–August 1937	110	?	(?)	41	(37.2)	?	(?)
B	Bering Strait	May–June 1952–58	49	7	(14.3)	17	(34.7)	25	(51.0)
C	Bering Strait	May–June 1961–68	171	31	(18.1)	62	(36.3)	78	(45.6)
D	Chukchi Sea	July–Aug 1972–73	201	23	(11.4)	87	(43.3)	91	(45.3)
E	Bristol Bay	March–April 1976	34	5	(14.7)	15	(44.1)	14	(41.2)

[a] Sources: A = Freiman (1941); B = J. W. Brooks and K. W. Kenyon (unpublished data); C = Burns (1965 and unpublished data); D = Gol'tsev (1975); E = Gol'tsev (1978 and unpublished data).

[b] Females of breeding age that had ovulated at least once: barren = neither pregnant nor having recently given birth; pregnant = having an unimplanted blastocyst or an implanted embryo or small fetus; bearing = having a near-term fetus or recently (within 4 months) given birth to a calf.

that, whereas there may have been no conscious selection for females with calves, these samples probably were drawn from herds in which such animals prevailed. Because there is some mortality of fetuses, birth rate should tend to be lower than pregnancy rate in representative samples. Data on rates of reproductive success have indicated that only about 83% of ovulations and 95% of conceptions result in live births (Table 35).

Samples B and C in Table 47 are known to have been drawn mainly from "nursery herds," which would account for their apparent overrepresentation of cows bearing calves. I am confident that the fifth sample (E) was not biased in the same way, because it was taken early in the spring, before the nursery herds were formed. The probability of bias in the two samples from the Chukchi Sea (A, D) is unknown to me, but I suspect that overrepresentation of cows bearing calves is likely to be consistently high in harvests taken during spring and summer, simply because exploitation of large rather than small herds is most efficient in returns vs. time expended.

These are the best empirical data available for estimation of gross productivity, but the birth rates suggested by them probably are higher than those of the adult female population at large, because of overrepresentation from the nursery herds. The pregnancy rates probably were not affected by the same bias, however, for pregnant females tend to be less gregarious and are uncommon in the nursery herds. Nevertheless, the pregnancy rates require some adjustment, because they were not derived by the same methods. The age compositions of the samples also need to be compared, since both fertility and fecundity vary with age (Krylov 1962; Burns 1965). A sample made up mainly of young adults will tend to show a higher pregnancy rate than one made up of older animals (Tables 34, 35).

The age compositions of samples B, C, and E of Table 47 are known in part; that of D is unknown; the composition of sample A can be derived from the given body and tusk size classes relative to body and tusk growth curves (Figs. 19 and 81). Comparison of the age compositions of samples A to E with an ostensibly random sample of females reported by Krylov (1968: Table 7), indicates (Table 48) that they are sufficiently similar to be accepted as representative of the females of breeding age. I assume that sample D also is representative.

Table 48. *Comparison of age compositions of the samples in Table 47 with an ostensibly random sample of females of breeding age reported by Krylov (1968).*

	Sample and (in parentheses) sample size									
	A (110)		B (20)		C (153)		E (33)		Random (32)	
Age class (years)	No.	%	No.	%	No.	%	No.	%	No.	%
6–9	24	22	9	45	38	25	5	15	7	22
10–15	39	35	9	45	70	46	18	54	13	41
16–20	31	28	1	2	30	20	7	21	8	25
>20	16	14	1	2	15	10	3	9	4	12

Table 44. *Numbers of walruses in the St. Lawrence Island (SLI) and Bristol Bay (BB) areas in relation to the zones of relative distributional density recognized by Kenyon (1972).*

		Composition per distributional density zone[a]							
		SLI high		SLI low		BB low		BB high	
Sample type	Date	M	FY	M	FY	M	FY	M	FY
Aerial photos	April 1972	40	1,131	—	—	22	76	16	507
Shipboard observations	April 1971	13	319	184	8	56	7	—	—
Shipboard observations	March 1972	90	817	—	—	—	—	—	—
Shipboard observations	March 1976	—	—	—	—	54	19	—	—
Totals		143	2,267	184	8	132	102	16	507
Percentage within zone		6	94	96	4	56	44	3	97

[a] M = subadult and adult males (10 years and older); FY (females and young) = females of breeding age (6 years and older) with immature males (<10 years) and females (<6 years).

as in the 1960 population. It resembles the estimated composition of the 1960 population in that about 75% of the females were of breeding age (6 years and older), and about 27% of the males were mature adults (15 years and older). The principal difference between the two estimates is that the overall sex ratio of males to females derived for the 1960 population was near unity, whereas the ratio for the 1972 population was disproportionate (Table 46). That females could have been considerably more numerous than males in 1972 seems

Table 45. *Estimated composition of the Pacific walrus population in 1972.*[a]

	Age class (years)			
Sex and density zone	0–9	10–14	>14	Total
Males				
St. Lawrence high	11,420	360	3,200	14,980
St. Lawrence low	115	8,600	5,050	13,765
Bristol Bay low	1,420	5,550	3,260	10,230
Bristol Bay high	6,845	100	930	7,875
Total	19,800	14,610	12,440	46,850
	0–5	>5		
Females				
St. Lawrence high	11,420	32,880		44,300
St. Lawrence low	115	340		455
Bristol Bay low	1,420	4,080		5,500
Bristol Bay high	6,845	19,690		26,535
Total	19,800	56,990		76,790

[a] Numbers of animals based on estimate of 123,640 overall and zonal proportions derived by Kenyon (1972).

Table 46. *Comparative percentage compositions inferred for the 1960 and 1972 populations of Pacific walruses.*[a]

Sex and age (years)	Year 1960	Year 1972
Males		
0–9	21	16
10–14	15	12
>14	14	10
Total	50	38
Females		
0–5	12	16
>5	38	46
Total	50	62

[a] From Tables 43 and 45.

consistent with known events. The catches and losses in the harvests after 1958 were made up of about 75% males and 20% females, which probably could have created an imbalance in the overall sex ratio tending to favor the females.

The sex ratio of the breeding adults has been a point of contention between Soviet and American biologists in recent years. Whereas Chapskii (1936) estimated it as 1 male:3 females, his successors in the Soviet Union (Fedoseev 1962; Krylov 1968; Fedoseev and Gol'tsev 1969; Gol'tsev 1975) and some North American workers (Mansfield 1958*a*; Burns 1965) have assumed that the ratio of adults was 1:1, like that of the newborn calves. In the estimated compositions derived herein, the implied ratio of breeding adults is about 1 male:3 females to 1:5, which is consistent with those of other polygynous pinnipeds (*Arctocephalus* 1:5, Rand 1972; *Zalophus* 1:4, Peterson and Bartholomew 1967; *Mirounga* 1:2-1:3, Le Boeuf 1974; *Halichoerus* 1:4-1:5, Anderson et al. 1975). Since male walruses require about 15 years to reach full maturity, whereas most females mature by age 6 or 7, it is possible that the number of females of breeding age could be about double the number of mature males, even if their survival rates were equal. Because the mortality of males of other polygynous species tends to be greater than that of the females (Chapman 1964; Johnson 1968; Le Boeuf 1974), this probably is true also of walruses. If so, the overall sex ratio in an unexploited population would be expected to include more females than males, and the sex ratio of breeding adults would be highly disparate.

Production

The gross productivity of walruses is substantially lower than that of other pinnipeds, because the females ordinarily reproduce at intervals of 2 years rather than 1 year. Hence one would expect the birth rate to be about half that of species which reproduce annually.

Several recent harvest samples from the Pacific walrus population in which there was no selection for females with calves showed pregnancy rates of 35 to 44% and birth rates of 41 to 51% in females of reproductive age (Table 47). The fact that the birth rates were mostly higher than the pregnancy rates indicates

Table 43. *Estimated composition of the Pacific walrus population in 1960.*[a]

Sex and locality	Herd type	Age class (years)				
		0–5	6–9	10–14	>14	Total
Males						
W. Bering	All-male	1,020	3,125	1,960	1,160	7,265
W. Chukchi	All-male	755	1,510	3,395	3,775	9,435
W. Chukchi	Mixed	1,230	610	1,285	645	3,770
W. Chukchi	Female	1,605	0	0	0	1,605
E. Bering	All-male	240	330	930	1,500	3,000
E. Chukchi	Mixed	390	210	420	210	1,230
Total		5,240	5,785	7,990	7,290	26,305
		0–5		>5		
Females						
W. Chukchi	Mixed	1,015		4,415		5,430
W. Chukchi	Female	4,825		13,670		18,495
E. Chukchi	Mixed	330		1,440		1,770
Total		6,170		19,525		25,695

[a] Numbers of animals based on the estimate of 46,000 in Soviet waters (Fedoseev 1962) and assumption of 6,000 in Alaskan waters in late summer.

St. Lawrence Island and in Bristol Bay. Around each concentration were large areas containing widely scattered individuals and small groups (Fig. 138). From aerial photographs taken during that survey by D. A. Borchert and from observations made during three expeditions on icebreaking vessels in those high- and low-density zones, 3,344 animals were classified by sex and relative age (Table 44). At least 90% of the males in the high-density zones were judged to be mature (>14 years), whereas only about one-third of those in the low-density zones were mature. In a random sample of 116 males from the Bristol Bay low-density zone in March–April 1976, males 15 years old and older made up 37% (V. N. Gol'tsev and F. H. Fay, unpublished data). Counts of 853 females and young, mainly in the areas of high density, indicated that 507 (59%) were females of breeding age and 346 (41%) were immature animals of both sexes, presumably with a 1:1 sex ratio (F. H. Fay, unpublished data).

Applying the above proportions and those in Table 44 to Kenyon's (1972) regional estimates of walrus numbers, a population with the following composition is inferred:

- In the St. Lawrence high-density zone, the total number of animals was estimated as 59,280. Of those, about 6% (3,560) were males 10 years old and older and 94% (55,720) were adult females and immature animals of both sexes. Of the males, 10% (360) were under 15 years old and 90% (3,200) were 15 years and older. Of the females and young, 41% (22,840) were immatures of both sexes and 59% (32,880) were adult females.
- In the St. Lawrence low-density zone, the total number of animals was estimated at 14,220. Of those, about 96% (13,650) were males 10 years and older

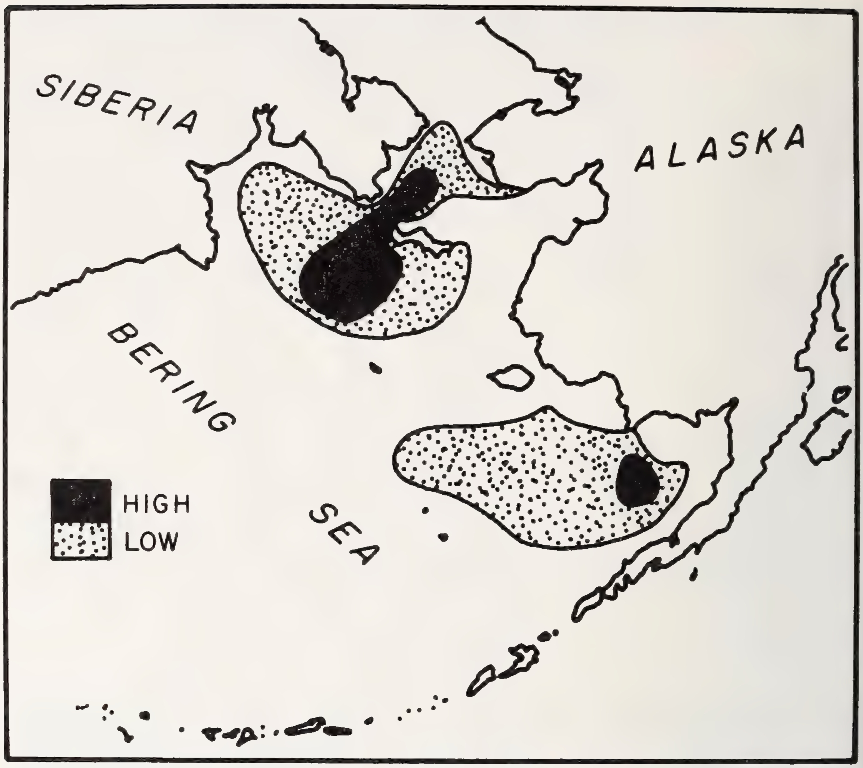


Fig. 138. High- and low-density zones of walrus distribution in the Bering Sea, April 1972. (Adapted from Kenyon 1972)

and 4% (570) were adult females and immature animals of both sexes. Of the males, 63% (8,600) were under 15 years old and 37% (5,050) were 15 years and older. Of the females and young, 41% (230) were immatures of both sexes and 59% (340) were adult females.

- In the Bristol Bay low-density zone, the total number of animals was estimated at 15,730. Of those, about 56% (8,810) were males 10 years and older and 44% (6,920) were adult females and immature animals of both sexes. Of the males, 63% (5,550) were under 15 years old and 37% (3,260) were 15 years and older. Of the females and young, 41% (2,840) were immatures of both sexes and 59% (4,080) were adult females.
- In the Bristol Bay high-density zone, the total number of animals was estimates at 34,410. Of those, about 3% (1,030) were males 10 years and older and 97% (33,380) were adult females and immature animals of both sexes. Of the males, 10% (100) were under 15 years old and 90% (930) were 15 years and older. Of the females and young, 41% (13,690) were immatures of both sexes and 59% (19,690) were adult females.

The composition derived from these estimates (Table 45) is imprecise, and its most obvious errors seem to be in the numbers of immature and subadult males, Sea were made up of somewhat older animals than those in the Gulf of Anadyr (Fedoseev and Gol'tsev 1969).

The remainder of the herds in the western Chukchi Sea were of two types: "mixed" herds, mainly of adult females and young of both sexes with a few older males, and "female" herds made up only of females with young of both sexes. About 31% of the animals were in mixed herds and 69% were in female herds (Krylov 1968: Table 4). The mixed herds, according to Krylov's (1966*a*) visual sample of 626 animals, were composed of about 21% males with bosses on the neck and shoulders (about 10 years old and older: Krylov 1967), 48% "adult" females (6 years old and older: Krylov 1966*b*), 20% immature males (under 10 years), and 10% immature females (under 6 years). Krylov (1966*a*) cited a comparable sample (size not given) recorded by P. G. Nikulin in 1952 of 16.7% adult males, 48.8% adult females, and 30.3% immature animals of both sexes in mixed herds in the Chukchi Sea.

The composition of the female herds was implied by a nonselective sample of 43 females taken in the Chukchi Sea in 1962 (Krylov 1968: Table 7). Of those, 26% were immature females (under 6 years), and 74% were breeding adults. Immature males were not mentioned but must have been equal to at least one-third the number of immature females, since young males also remain with the mother for at least the first 2 years and are gradually recruited into all-male herds over the next 4 or 5 years.

With these proportions, a crude approximation of the composition of the estimated 46,000 walruses in Soviet waters in summer 1960 (Fedoseev 1962) can be reconstructed, as follows:

- The animals in all-male herds made up 32 to 42% of those counted (Fedoseev 1962; Krylov 1968), the mean of which is (0.32 × 39,100) + (0.42 × 30,000) = 25,110/69,100 = 36.3% or about 16,700 animals.
- Of these, 43.5% (7,265) were in the Bering Sea and 56.5% (9,435) were in the Chukchi Sea (Krylov 1968).
- The composition of the Bering Sea all-male herds, according to Gol'tsev (1968) was about 14% (1,020) under 6 years old, 43% (3,125) 6 to 9 years old, 27% (1,960) 10 to 14 years old, and 16% (1,160) 15 years and older.
- The composition of the Chukchi Sea all-male herds, assuming that the younger age classes may have been underrepresented in the harvest samples (Fedoseev and Gol'tsev 1969), was about 8% (755) under 6 years old, 16% (1,510) 6 to 9 years old, 36% (3,395) 10 to 14 years old, and 40% (3,775) 15 years and older.
- The animals in the mixed and female herds made up 58 to 68% (mean, 63.7%) of the total, or about 29,300 individuals.
- Of those, 31.4% (9,200) were in mixed herds and 68.6% (20,100) were in female herds (Krylov 1968).
- The mixed herds comprised 41% males (3,770) and 59% females (5,430), according to Krylov (1966*a*). Of these, males less than 10 years old made up about 20% (1,840), probably at least two-thirds of which (1,230) were under 6 and the rest (610) were 6 to 9 years. Males 10 years and older made up 21% (1,930), of which probably about two-thirds (1,285) were 10 to 14 years and one-third (645) was mature adults 15 years and older. Females under 6 years made up 11% (1,015), and adult females 6 years and older were 48% (4,415).

- Of the 20,100 animals in female herds, the females alone were 26% immature (under 6 years) and 74% adults (Krylov 1968). But there must have been at least one-third as many immature males (under 6 years), as immature females. Hence, the overall proportions were about 8% (1,605) males under 6 years old, 24% (4,825) females under 6 years old, and 68% (13,670) adult females.

To these approximations must be added the walruses that were in Alaskan waters in late summer. Herd numbers and composition were not as well documented there, but it is clear that at least 3,000 males were using Bristol Bay (V. N. Crosby, personal communication), and it is probable that mixed herds of as many animals were in the eastern Chukchi Sea. From photographs of about half of the males on Round Island in 1958, I estimated their age composition as 8% (240) under 6 years old, 11% (330) 6 to 9 years old, 31% (930) 10 to 14 years old, and 50% (1,500) 15 years and older. These proportions are different from those given by Gol'tsev (1968) for the Rudder Spit herd. They have been confirmed, however, by Miller (1976: Table 5), who classified more than 3,000 males at Round Island in 1972–73 as 20% "small," 39% "medium," and 41% of "large" size. Although precise ages cannot be assigned to these size classes, Miller's "small" animals probably were less than 10 years old; the "medium"-sized individuals probably were between 10 and 15 years old; and the "large" individuals would have been mature adults more than 15 years old (cf. Miller 1975*a*: Figs. 2, 7, 8–11, 14).

I assume that the herds in the eastern Chukchi Sea were all of the mixed type and that their composition was comparable to that of mixed herds in Soviet waters, about 13% (390) males under 6 years old, 7% (210) males 6 to 9 years old, 14% (420) males 10 to 14 years old, 7% (210) males over 14 years old, 11% (330) females under 6 years old, and 48% (1,440) females 6 years and older.

On summing these estimates (Table 43), I infer that the population in 1960 was made up of about equal numbers of males and females. Immature males (up to 9 years) made up 21%, and immature females (up to 5 years) were 12%. Males of breeding age (10 years and older) made up about 29%; mature males 15 years and older were about 14%, and females of breeding age (6 years and older) made up about 38% of the population.

This reconstruction obviously is not accurate, for the number of males in the 10- to 14-year class should be smaller than that in the 0- to 5-year class. Also, one would expect the males and females in the 0- to 5-year class to be about equal. The somewhat smaller number of females than of males, overall, is consistent with Burns' (1965) estimation that the harvests before 1960 removed more females than males from the population.

Population in 1972

Proportional counts of walruses in their wintering areas in the Bering Sea were obtained in the early 1970's in conjunction with several aerial and shipboard surveys (F. H. Fay, unpublished data). By applying these proportions to Kenyon's (1972) median estimate of 123,640 animals in the population, the composition of the population in 1972 can be inferred.

Kenyon (1972) recognized from the results of his 1972 survey that the animals were unevenly distributed in the pack ice, being concentrated in the vicinity of enough answers are obtained to describe its basic size, structure, and demographic characteristics, the Pacific walrus population should be capable of providing a large, sustained harvest, without risk of repeating the mistakes of the past or neglecting the needs of the future.

Acknowledgments

The material in this report was gathered over 28 years, beginning in 1952, and the study received support from many sources during that period. In the 1950's, my work was aided mainly by funds made available through contractual arrangements between the U.S. Office of Naval Research and the Arctic Institute of North America under contract Nonr 1138(01). In the 1960's, it was supported principally in connection with the Animal-Borne Disease Program of the Arctic Health Research Center, Public Health Service, U.S. Department of Health, Education, and Welfare and by funds made available to that program through interagency agreement with the Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service. In the 1970's, it was aided in part by the University of Alaska Sea Grant Program, supported by NOAA Office of Sea Grant, U.S. Department of Commerce, under contracts GH–83, I–36109, and 04–3–158–41; in part by the Bureau of Land Management through interagency agreement with the NOAA Environmental Research Laboratories, Office of Alaskan Outer Continental Shelf Environmental Assessment Program; in part by the U.S. Marine Mammal Commission, under contracts MM4AC–006, MM5AC–024, and MM1533576–0; and in part by the State of Alaska with research funds made available through the Institute of Marine Science, University of Alaska. At various times, logistic support was provided by the U.S. Coast Guard, the U.S. Air Force, the U.S. Department of Interior's Bureau of Commercial Fisheries, Bureau of Sport Fisheries and Wildlife, and Bureau of Indian Affairs, the National Science Foundation's R/V *Alpha Helix* program, the Soviet Ministry of Fisheries through the Marine Mammal Project, US–USSR Environmental Protection Agreement, the New York Zoological Society, the Alaska Packers Association, and by the Eskimos of St. Lawrence Island, Bering Sea.

A large number of people contributed their time and special knowledge during the course of this work. For providing the initial inspiration and direction, I am particularly indebted to I. McTaggart Cowan of the University of British Columbia, V.B. Scheffer of the Bureau of Commercial Fisheries, and R. F. Scott and J. P. Kelsall who were my fellow students at the University of British Columbia. For many years subsequent to that, I was encouraged and aided by those people and especially by K. W. Kenyon of the Bureau of Sport Fisheries and Wildlife, R. L. Rausch of the Arctic Health Research Center, J. J. Burns of the Alaska Department of Fish and Game, and my wife, B. A. Fay.

Among the many others who contributed information, services, and other forms of assistance were D. P. Abbott, M. Arnow, E. D. Asper, C. A. Barnes, F. M. Bayer, R. Baxter, M. A. Beal, B. J. Benchley, W. Benton, D. A. Borchert, H. W. Braham, J. G. Bridgens, J. W. Brooks, D. H. Brown, J. L. Buckley, IU. A. Bukhtiarov, T. J. Cade, W. W. Caldwell, W. M. Cameron, W. Carroll, T. D. Carter, F. A. Chace, Jr., J. Clarke, V. N. Crosby, J. M. Cuthill, H. DeVoe, R. A. Dieterich, J. P. Dittmer, M. J. Dunbar, J. A. Estes, J.

Faro, V. R. Farrell, G. A. Fedoseev, H. W. Ferren, C. H. Fiscus, H. D. Fisher, R. H. Flemming, A. French, K. J. Frost, R. Galleher, O. W. Geist, J. R. George, R. B. Gibson, R. M. Gilmore, V. N. Gol'tsev, F. Goro, K. Grauvogel, D. Gray, R. F. Gray, S. J. Harbo, J. Harkey, R. Hajny, A. C. Heinrich, J. E. Hemming, C. A. Hill, A. Hopson, C. C. Hughes, M. L. Johnson, R. D. Jones, Jr., B. P. Kelly, A. A. Kibal'chich, J. G. King, D. R. Klein, E. Knudtsen, R. M. Laws, E. M. Little, A. G. Loughrey, W. K. Lyon, E. T. Lyons, S. McCutcheon, J. McGraw, R. McLaughlin, I. A. McLaren, D. J. McLean, C. P. McRoy, S. McVay, R. Mahaffey, A. W. Mansfield, H. F. Meyers, E. H. Miller, R. V. Miller, E. D. Mitchell, Jr., G. Mower, E. Muktoyuk, O. J. Murie, F. Neave, R. Nelson, R. Niesz, T. J. O'Brien, J. D. O'Donahue, R. S. Peterson, K. W. Pitcher, W. E. Rasmussen, V. R. Rausch, H. A. Rehder, C. A. Repenning, D. G. Ritter, R. A. Ryder, J. Sarvis, K. B. Schneider, H. C. Scudder, D. E. Sergeant, D. Shinen, C. R. Shoemaker, W. Sholes, L. M. Shults, O. Siebert, A. W. Smith, C. A. Smith, D. L. Spencer, I. Stirling, S. W. Stoker, J. Taggart, L. Temple, A. Thayer, S. H. Thompson, T. Thoreson, P. E. Tovey, R. Tremaine, R. Trites, J. R. Twiss, Jr., J. Waite, G. E. Watson, N. Whitaker, F. Wilke, F. S. L. Williamson, G. S. Wilson, C. Vibe, P. Viereck, and C. Zabel.

In the preparation of this report, I have benefited greatly from constructive reviews by J. J. Burns, D. G. Chapman, D. K. DeMaster, L. L. Eberhardt, H. M. Feder, K. R. Gordon, R. J. Harrison, R. J. Hofman, L. Irving, A. W. Johnson, B. P. Kelly, K. W. Kenyon, J. K. Ling, L. F. Lowry, C. P. McRoy, E. H. Miller, R. L. Rausch, C. E. Ray, G. C. Ray, C. A. Repenning, D. W. Rice, V. B. Scheffer, R. B. Weeden, and F. S. L. Williamson on major parts of earlier drafts.

Much of the success and pleasure of this work was derived from close association with the Eskimo walrus hunters of St. Lawrence Island, who gave liberally of their time and facilities, in return for no more than my labor and the satisfaction of my curiosity. For their patience, unflagging enthusiasm, and willingness to share their resources and expertise with me, I shall be ever grateful. I dedicate this volume to them, with the hope that it will bring pleasure, unexpected enlightenment, and the satisfaction that their contributions were not in vain.

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January–February, as implied by the data presented here? Do the females in first estrus ovulate at a different time than the others? What is the normal bull:cow ratio in the mating groups? How many cows does one bull service? Does mating take place in specific localities, year after year? Does mating take place in the water or on the ice? Do the near-term pregnant cows mix with the mating groups or remain segregated from them? What is the nature of the competition between bulls for the estrous cows? Does each bull remain with a specific group of cows; if so, for how long? Do the cows in that group stay together throughout the mating season, or is there free interchange between groups? How old are the bulls that take part in the mating? As the older bulls go out of rut and the younger bulls come in, is there gradual replacement by successively younger breeders? Do the bulls feed during the rut? Is the social organization during the postpartum estrus in summer comparable to that in the winter mating season?

Information is also needed concerning the time and place of calving and the circumstances during birth and early nurture of the calves. Is the peak of calving really in mid-May? What proportion of calves is born outside the main calving season? Do all births take place on the ice? How soon after birth do the calves enter the water? In what areas does calving take place? Does the cow usually give birth within or apart from the herd? Why do the cows with new calves tend to form large nursery herds, rather than remaining separate or in small groups? Why do they not join non-nursery groups? How strong is the social bond between cow and calf, and what are the circumstances under which it is broken? How important is fosterage to calf survival? Do foster parents feed their adopted calves? How much exchange of calves takes place in the nursery herds? Why do cows with new calves not use the coastal hauling grounds, with the bulls? What is the principal function of the unusually prolonged cow–calf bond?

Because most of the data presented on reproduction in this report were obtained during periods of suppression and rapid recovery of the population, they may not apply to the population at or near maximum size. How will the rates of ovulation, conception, and birth change as the population approaches the maximum? Will the net productivity decline as a result of reduced reproductive effort, increased prenatal mortality, or lowered survival of the young? Will the increased proportion of old animals in the population result in lowered production through semi-senility?

As yet little quantitative information is available on the feeding habits of these animals outside the St. Lawrence–Bering Strait area, and most of that was obtained in late April to early June. Practically nothing is known about their feeding in the main wintering areas, very little about it in the summering areas, and nothing during the autumn migration. How important is it to these animals to have available a copious supply of bivalve mollusks? Can they get by with alternate kinds of prey? Do some of their prey contain essential nutrients not found in the rest? Do some prey have optimal nutritive value only in certain seasons? Why do the organisms eaten by females tend to be much smaller than those eaten by males? Is this the rule in all areas, in all seasons? What proportion of the dietary intake by the suckling young is made up of benthic invertebrates by the end of the first year? By 18 months? Do they eat the same kinds of organisms as the adults at that time? If a walrus removes the siphon alone from a clam, can the clam regenerate its siphon? How much digging does a walrus need to do to obtain its daily food? Does that bioturbation have a beneficial or detrimental influence on the rest of the fauna in that system? Does it result in a significant release of nutrients that would otherwise be entrapped forever? Why do some walruses feed on the flesh of other marine mammals? Is this a seasonal event or does it take place to some extent in all areas, in all seasons? Do the walruses feed only on carrion, or do they actually pursue and kill other pinnipeds? Do they ever cannibalize their own kind? Are blubber thickness and composition good indicators of the kinds and quantities of prey eaten on a seasonal and regional basis?

Until a great deal more is known about the causes and age-specific rates of natural mortality, the managers will have little hope of accurately estimating the appropriate size of harvests. The mortality from predation will be the most difficult to assess, for the animal that is consumed entirely is not readily accountable. Can predation by polar bears be assessed by searching the ice for remains, especially the tough hides which the bears apparently do not eat? Some of the animals that die from other causes eventually drift ashore. Can their age, sex, and cause of death be determined in samples large enough to provide insight into the impacts of those causes on the population? Can counts of sex–age composition, especially of the younger age classes, provide adequate estimates of survivorship and recruitment? Why is there mass mortality in autumn each year on the Punuk Islands hauling ground and not on other haulouts?

The managers will require better estimates of population size or relative size and must have more realistic estimates of its composition than are presently available. Further studies of the behavior of the animals, especially of their activity budgets, feeding rhythms, surface:subsurface times, and responses to weather and ice conditions appear to be essential for refinement of census methods and for interpretation of the results. Can the numerical status of the population be monitored more efficiently by annual inventory of animals using traditional hauling grounds? Can a mark–recapture system be developed and implemented to provide an estimate of population size? Can the indirect biological indicators of population status (such as blubber thickness, serology, incidence of disease, reproductive rates, and growth rates) be monitored adequately by sampling the native harvests? How can a reliable estimate of composition of the population be obtained?

From the ecological aspect, much more information is needed, for example, on the distribution, community structure, standing stocks, and turnover rates of the principal prey. What are their food chains and what are the oceanographic processes on which they rely? Who are the walrus' principal competitors for those prey? How important are they to the walrus? How do those competitors interact with other components in the system? How does the variation in extent of the winter ice, which is an important substrate for epontic algae, affect the growth and productivity of the walrus' filter- and detritus-feeding prey? How important in general are those epontic algae to the food chains of the walrus' prey? How does the winter ice affect the distribution of walruses, their prey, their predators, and their competitors? How much influence do weather and ice conditions exert on the walrus' success in mating, calving, and survival of the young?

Clearly, the answers to most of these questions will not be easily obtained. If

Table 50. *Comparison of observed numbers of 1- and 2-year-old young with predicted numbers of calves in two samples of fertile females in the Bering Sea.*

		Number of individuals			
Time	Location	Adult females	Calves[a]	1 year old	2 years old
May–June 1954	St. Lawrence I.	52	19	21	17
March–April 1976	Bristol Bay	14	5	3	5
Total		66	24	24	22

[a]Estimated from mean birth rate of 36.7% for adult females (Table 49).

age in both sexes. Presumably, the mortality of males from natural causes, as well as from the harvests, is greater than that of females at all ages.

If the survival in the first 2 years is about 80%, as suggested by Chapskii (1936), and no less than 90% per year for the next 6 or 7 years, as suggested by the low value (0.16 to 0.2) of F, the female birth rate (Eberhardt and Siniff 1977: Fig. 2), then the recruitment of females from birth to breeding age could be about 40 to 50%. Since the males do not reach maturity until they are about 15 years old, well after they enter the harvest, and because their survival rate probably is lower than that of females, I suspect that the recruitment of males from birth to maturity is no greater than about 10 to 20%.

Burns (1965) estimated that the net annual increment to the population after natural and harvest mortality was only about 1% in the early 1960's. Conversely, Fedoseev and Gol'tsev (1969) estimated a net loss and concluded that the population was still declining. Probably both of those estimates were very conservative, for the aerial censuses and distributional data suggest a marked increase in population size in recent years. The rate and magnitude of that increase, however, are unknown.

Outlook

The Pacific walrus population at present seems to be very large, very productive, and very secure under the current harvest system, but there are a number of uncertainties about its future. Foremost of these, in my opinion, is the biopolitical question of how and by whom the population will be managed. At present, responsibility for management of the population and of the resources with which it interacts rests equally in the hands of the governments of the United States and the Soviet Union, between which there is a considerable communication gap. Some progress has been made in recent years in bridging that gap through cooperative interchange under the Marine Mammal Project (V.6.1) of the US–USSR Environmental Protection Agreement of 1972, but the fact remains that each nation still manages the resources within its own jurisdictional boundaries on a unilateral basis. The marine system of the Bering and Chukchi seas and the renewable resources therein do not lend themselves to such partitioning. The Pacific walrus population is a prime example, in that it resides in winter mainly in American waters and in summer principally in waters under

Soviet control. The walrus population is shared equally between these two nations, as are the resources on which it depends. Hence, management of the walrus and of its environment, should not be the prerogative of either nation but of both, on a highly cooperative basis. Until such cooperation is assured through international convention, the future of the walrus population and other resources of the Bering and Chukchi seas seems uncertain.

Over the past 28 years (1952–79), I have observed a remarkable evolution of management and research goals associated with the Pacific walrus. In the beginning there was intensive protection by the American government and overexploitation by the Soviets, each without adequate knowledge of the animals or their environment. This was followed by rigid protection on the Soviet side and close management by the Americans, based on the single-species approach in which the walrus was studied as an autonomous creature, disconnected from its supporting environment. Finally, the synecological approach was developed, in which the walrus is recognized as an integral part of the entire system in which it lives. System-wide management, with due acknowledgment of the interrelations of all of its parts and for maintenance of their balance, still is an ideal or goal, rather than a practice, for the inner workings of the Bering–Chukchi system are not yet fully understood.

Over those 28 years, my colleagues, co-workers, and I have learned much about the biology and ecology of the Pacific walrus. As can be seen in the foregoing report, however, much more needs to be learned about this mammal, as well as about the environment of which it is a part, before that ideal of ecosystem management will be feasible.

Concerning the distribution and migrations, we can infer some general pattern to the seasonal use by walruses of the Bering and Chukchi seas, but we still know very little of their specific migration routes, rates of passage along those routes, or the fidelity of individuals to specific areas. Walruses would be unusual among pinnipeds if they did not show some fidelity to mating and calving areas and to migration corridors, at least in a general way (cf. Carrick et al. 1962; Peterson and Bartholomew 1967; Peterson 1968; Stirling 1971; Le Boeuf 1974; Mansfield and Beck 1977). If they are site fidelitous, then we need to know much more about the nature of the major wintering concentrations and their contributions to harvests along the migration routes. Since the mating of walruses appears to take place in mid-winter to late winter when these major concentrations exist, can we assume that each concentration is a semi-isolated reproductive unit, possibly requiring separate management consideration? Do these wintering units mix on the summering grounds in the Chukchi Sea? Do they compete for resources at that time, although they appear to be noncompetitive in winter? Is the sex–age composition of animals wintering in each area similar to that in the others? Is there sufficient interchange between them to insure that depletion of one unit will be replenished by the other? Are the summering males at Round Island and Rudder Spit most of the breeding bulls from the Bristol Bay and St. Lawrence concentrations, respectively? Are the bulls that go north with the females in spring the ones that have not participated in mating?

More information is needed about the time and place of mating and the reproductive behavior at that time. For example, do most of the females ovulate in

Adjustment of the sample pregnancy rates in Table 47 is required because the specimens were taken in different months, and the criteria for identification of pregnancy were not uniform. "Pregnant" animals in samples B, C, and E were identified by the presence of a large corpus luteum in the ovaries, because most of them were taken before implantation of the blastocyst. Conversely, samples A and D were taken after implantation, and the animals were identified as pregnant by the presence of a conceptus. Because there is some failure in fertilization, conception, and gestation, as noted earlier, the presence of a corpus luteum early in pregnancy is not equivalent to presence of a conceptus later; neither of these is equivalent to live birth.

The mean difference between ovulation and conception rates has been estimated as about 12.5% (Table 35). I have assumed that the mortality of shed ova and blastocysts is evenly distributed over a 5-month pre-implantation period (1 February to 1 July) and have adjusted the pregnancy rates of samples B, C, and E accordingly, to obtain the equivalent of conception rates (Table 49). Because samples A and D were taken at or soon after implantation, their pregnancy rates are tantamount to conception rates and require no adjustment.

The derived conception rates range from about 34 to 43% per year (mean, 38.7%). Because the mean difference between conception and birth rates is about 5.2% (Table 35), the most probable adjusted birth rates of the samples would range from about 32 to 41% (mean, 36.7%) per year (Table 49). If the population as a whole in 1960 included 38% females of breeding age (Table 43) its crude birth rate would have been between 12 and 16% (mean, 14%) per year. If the population in 1972 included 46% females of breeding age, its crude birth rate would have been between 15 and 19% (mean, 17%) per year.

Table 49. *Adjusted sample rates of conception and birth in samples A to E of fertile females from Table 47.*

Sample	Sample size	Conception		Birth	
		No.	%	No.	%
A	110	41	37.2	38.9	35.4
B	49	16.6	33.9	15.7	32.0
C	171	60.4	35.3	57.2	33.4
D	201	87	43.3	82.5	41.0
E	34	13.9	40.9	13.2	38.8
Total	565	218.9	38.7	207.5	36.7

Survival and Recruitment

The unusually low reproductive rate of walruses must be balanced by lower mortality and a higher recruitment to breeding age than in other pinnipeds. The unusually long period of parental care (2 years) probably is a major factor contributing to that high survivorship. Loughrey (1959) estimated that recruitment to breeding age in the Canadian walrus population amounted to about 10% per year; Mansfield (1966) implied that recruitment was somewhat greater than 6% per year. Krylov (1963) estimated the recruitment rate of Pacific walruses to breeding age at 6.3% per year; Fedoseev and Gol'tsev (1969) estimated that recruitment did not exceed 9% per year.

Other gregarious and polygynous pinnipeds, such as the gray seal (*Halichoerus grypus*), elephant seal (*Mirounga* spp.), and northern fur seal, show survival of young during the first year ranging from about 40 to 85% (Hewer 1957, 1964; Laws 1960; Chapman 1964; Mansfield and Beck 1977), apparently being highest when population density is low. Survival during the second (70 to 86%) and third years (80 to 90%) tends to be still higher. Survival rates in those species generally are highest (85 to 90%) over the next 5 or 6 years, then decline steadily thereafter. Survival of males tends to be slightly lower than that of females in the first 6 to 8 years and to be much lower thereafter.

I assume that specific mortality of walruses changes with age in a manner comparable with those of the other polygynous pinnipeds. Certainly, the mortality from intraspecific traumatization is greater in calves than in any of the older age classes (Fig. 129). Mortality of calves also is higher than that of nearly all other age classes in the harvests. Furthermore, calves seem to be the primary targets of natural predators, such as killer whales and polar bears; probably they also are more subject to disease and thermal stress than the older animals.

Some indication of the mortality of calves in the perinatal period (April–June) is provided by data obtained by J. J. Burns and me from the Eskimo's harvests at St. Lawrence and Little Diomede islands in spring 1952–68. Of 148 fertile females that had recently given birth, 135 (91%) were accompanied by healthy calves; 13 (9%) had lost their calves at or soon after birth. Although this suggests that about 9% of the calves had died, we found at the same time seven other calves with foster mothers. If some of those were the lost calves, then the proportion that died may have been less than 9%. In a sample from the Chukchi Sea in July–August 1978, A. A. Kibal'chich (unpublished data) found 40 (34.5%) of 116 adult females accompanied by calves of the year. The predicted mean number of calves born to a sample of this size (116 × 0.367) would be 42 to 43, suggesting that about 5 to 7% mortality had taken place in the first 2 to 3 months after birth. The perinatal mortality of young of other polygynous pinnipeds evidently varies widely in relation to population density, being as low as 2 to 3% in populations that are still in the rapid growth phase, and as high as 13 to 60% in those near maximum size (Laws 1953*b*; Kenyon et al. 1954; Summers et al. 1975; Le Boeuf and Briggs 1977).

In their estimate of population composition, Fedoseev and Gol'tsev (1969) assumed that the survival of walrus calves to 1 year of age was between 65 and 73% by analogy with other pinnipeds, but they believed that the actual rate might be somewhat higher. Chapskii (1936) estimated from the calf:cow ratio of a nonselective harvest sample taken in the Kara Sea that the survival of young from birth to 2 years was about 80 to 82%. My results from two small samples counted in the Bering Sea (Table 50) lend support to Chapskii's (1936) estimate, but the sample size is too small for reliability.

The underrepresentaton of animals 1 to 6 or 7 years old in both the harvests and the natural mortality from intraspecific trauma (Figs. 127, 129) suggests that the specific survival rates of those animals probably are the highest of any age classes. Survivorship appears to decline markedly after about 8 to 10 years of

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Mammals of the La Selva–Braulio Carrillo Complex, Costa Rica

NORTH
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FAUNA

Number 75

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

North American Fauna

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ISSN 0078-1304

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Mammals of the La Selva–Braulio Carrillo Complex, Costa Rica

by

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Don E. Wilson
Barbara L. Clauson
Richard K. LaVal
Christopher S. Vaughan

NORTH
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Mammals of the La Selva–Braulio Carrillo Complex, Costa Rica

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ABSTRACT: Costa Rica's La Selva-Braulio Carrillo complex encompasses a 60-km protected corridor of Caribbean rain and cloud forest extending from 30 m at the La Selva Biological Station to 2,906 m at the top of Volcán Barva. The 52,000-ha complex covers four life zones and two transitional zones, including tropical wet forest, tropical wet forest cool-transition, tropical premontane wet-transition rain forest, tropical premontane rain forest, lower montane rain forest, and montane rain forest. Located in the northeastern part of the country, the area is representative of Central American Caribbean slope forests that extend from Mexico to Panama. The extensive elevational gradient of the complex provides protected habitat for a variety of altitudinal migrants.

With support from the National Geographic Society and Rice Foundation, the Organization for Tropical Studies organized a biological survey of the complex in early 1986. The mammal team worked at six sites along the elevational transect established by the expedition: 300 m, 700 m, 1,000 m, 1,500 m, 2,050 m, and 2,600 m. We supplemented our collecting records with unpublished records made available by colleagues, records in the published literature, and specimens in museum collections. In addition, observations recorded by a variety of observers at the La Selva Biological Station are summarized.

The mammal fauna of the complex comprises 142 species including 79 bats, 23 rodents, 15 carnivores, 7 marsupials, 6 edentates, 4 artiodactyls, 3 primates, 2 rabbits, 2 shrews, and 1 perissodactyl. At least 10 additional species are likely to occur there. The only species of mammal likely to have been extirpated from the area is the giant anteater.

Recognizing the importance of the area to wildlife and to mankind in general, the government of Costa Rica added 13,500 ha to the complex on 13 April 1986. This area, previously known as the ''Zona Protectora,'' provided the mid-elevational link between the lowlands of the La Selva Biological Station and the montane forests of Braulio Carrillo National Park. Unfortunately, destruction of the rain forests surrounding the complex will soon render it an isolated island of protected forest. Thus, the area will become increasingly valuable as a refuge for many species with home ranges that require extensive tracts of undisturbed habitat.

RESUMEN: El complejo La Selva–Braulio Carrillo de Costa Rica abarca un pasillo protejido de 60 kilómetros de bosque pluvial y selva nublada del Caribe. Extendiendose desde 30 metros sobre el nivel del mar, en la Estación Biológica de La Selva, hasta 2,906 metros, en la cima del Volcán Barva. El complejo de 52,000 hectáreas cubre cuatro zonas de vida y dos zonas de transición, incluyendo bosque húmedo tropical, bosque húmedo tropical con transición fría, bosque pluvial tropical pre-montano con transición húmeda, bosque pluvial pre-montano tropical, bosque pluvial montano-bajo, y bosque pluvial montano. Localizada en la parte noreste del país, el área es representativo de los bosques con pendiente de America Central y el Caribe que se extienden desde México hasta Panamá. La extensa gradiente de este complejo brinda lugares protejidos para una variedad de migrantes altitudinales.

Con el apoyo del National Geographic Society y Rice Foundation, la Organización de Estudios Tropicales organizó un estudio biológico del complejo a principios de 1986. El equipo trabajó en seis puntos de interés a lo largo del corte transversal de elevación establecido por la expedición: 300 m, 700 m, 1,000 m, 1,500 m, 2,050 m, y 2,600 m. Nosotros suplementamos nuestros archivos de colección con archivos inéditos puestos a la disposición por colegas, archivos en la literatura publicada, y especímenes en colecciones de museos. Además, se resumen las observaciones anotadas por una variedad de observadores en la Estación Biológica de La Selva.

La fauna mamífera del complejo consiste de 142 especies incluyendo 79 murciélagos, 23 roedores, 13 carnívoros, 7 marsupiales, 6 edentatas, 4 artiodáctilos, 3 monos, 2 conejos, 2 musarañas, y 1 perisodáctilo. Es probable que por lo menos diez especies adicionales se encuentra allí. El único mamífero que probablemente fue extirpado de este área es el oso caballo.

Reconociendo la importancia del área para animales y el género humano en general, el gobierno de Costa Rica añadió 13,500 hectáreas al complejo el 13 de Abril de 1986. Este área, previamente conocido como la ''Zona Protectora,'' suministró el eslabón de la elevación media entre la tierra baja de la Estación Biológica de La Selva y el bosque Montano del Parque Nacional Braulio Carrillo. Desafortunadamente, la destrucción del bosque

húmedo que circunda el complejo pronto se transformará en una isla aislada de bosque protejido. Así, el área se volverá cada vez más valiosa como refugio para muchas especies que necesitan espacios grandes en que el habitat no ha sido perturbado.

Costa Rica, with an area of 51,022 km^2, is a small country, but one of almost unparalleled biotic diversity. Within the country's borders there are more than 12,000 species of plants, including 1,200 species of orchids and 2,000 tree species. Costa Rica has more than 1,200 species of butterflies, more than are known from all of Africa. There are some 150 species of amphibians and more than 212 species of reptiles. More than 850 species of birds have been found in Costa Rica; this represents 10% of the world's species and more than have been found in the United States and Canada combined. The native mammal fauna consists of at least 200 species, all of which still can be found within the country's borders. The human population of Costa Rica numbered 2.7 million in 1988 and is increasing at a rate of 2.6% annually. Predictably, man and nature have come into direct conflict in recent years.

On his fourth and final voyage to the New World in 1502, Christopher Columbus became the first European to land on what the Spanish later termed the "Rich Coast," Costa Rica. At the time of the Spanish conquest in the early 1500's, primary forests covered an estimated 49,000 km^2 or 96% of the national territory. This land cover consisted of tropical dry forest, tropical moist forest, tropical wet forest, tropical premontane moist forest, tropical premontane wet forest, tropical premontane rain forest, tropical lower montane moist forest, tropical lower montane wet forest, tropical lower montane rain forest, tropical montane wet forest, and tropical montane rain forest (Holdridge 1967; Hartshorn 1983). Remaining land cover may have included tropical subalpine rain paramo and savannah. The extent of indigenous deforestation is unknown, but has been considered minimal. This may not be true however, as there is increasing evidence that rather dense populations of Indians lived in the Atlantic lowlands.

The primary settlers of the northern Caribbean lowlands of Costa Rica were individual families of European descent, the "campesinos." Land was cleared by individuals working with hand tools. Large tracts of intact forest remained in this area as late as the early 1970's. In the late 1970's and early 1980's habitat destruction in this region occurred at a significantly higher rate. This was due in part to increased human population densities and the availability of chain saws. However, perhaps of greater effect were two economic factors: (1) the increased need for and value of lumber as a building material within Costa Rica; and (2) the soaring international market for beef combined with the discovery that African cattle (Zebu, *Bos indicus*) would prosper in this region when the forest was cleared and introduced grasses planted.

By 1940, 15,000 km^2 of the forested habitat of Costa Rica had been altered. During the following 37 years, an additional 18,000 km^2 was deforested (Sader and Joyce 1988). Thus, more primary forest was destroyed between 1940 and 1977 than during the preceding 400 years (Oficina de Planificación del Sector Agropecuario 1979). By the 1960's, nearly 50% of the forest had been destroyed by logging and development. Today, less than 30% of the original forests remain in Costa Rica, and deforestation continues at the rate of 60,000 ha annually. Although reforestation efforts are beginning, most projects are still preliminary and account for less than 4,000 ha annually.

Tropical rain forests are the richest and most complex land biotas. Unfortunately, worldwide, more than half of what was formerly tropical rain forest has been destroyed by modern humans, and the rate of deforestation is increasing. Destruction of tropical forests is causing the extinction of thousands of species, many of them still unknown to science. Worldwide, between 76,000 km^2 and 92,000 km^2 of forest are being clearcut yearly and an additional 100,000 km^2 are being altered severely (Myers 1986). If this deforestation rate continues unchecked, an estimated 50% of existing tropical forests will be eliminated by the year 2000 (U.S. Department of State 1981). Mankind is losing the potential for the multiple use of these forests as sources of new drugs for medicines, food plants, genetic reservoirs, watersheds, recreational areas, and for sustained utilization of the biota, such as for hunting and logging. Additionally, destruction of large tracts of rain forest may affect continental weather patterns.

Habitat destruction and the associated loss of wildlife are not problems unique to the Caribbean lowlands of Costa Rica, but rather a global problem. It is especially acute in the tropics today as modern technology and demands for resources are putting humans and nature in direct conflict. It has been estimated that 60% of all species on the earth today will be extinct before scientists have a chance to study them. The establishment of protected reserves and parks, and the expansion of those that already exist, are critical if we are to preserve the flora and fauna of the planet. Nearly everywhere the boundaries of reserves are set by political expediency rather than on the basis of scientific data.

In Costa Rica, the only viable long-term solution for conservation of the biota is protection of remaining habitat and immediate research programs on sustained use. Most remaining forested lands form part of the more than 60 protected wildland areas, the majority of which are under governmental control. The Costa Rican National Parks Service has been outstanding in protecting wildlands, with more than 32 national parks and equivalent biological reserves protecting more than 500,000 ha of land or 12.5% of the national territory. Additionally, more than 9.6% of the national territory is protected in a combination of national forests and wildlife preserves and privately owned biological reserves. Unfortunately, the great majority of wildlands in Costa Rica are essentially unknown biologically; an obstacle to their efficient conservation and management. Additionally, many wildland areas are small and located in fragmented habitats; few reserves protect the continuum of altitudinal gradients necessary for survival of many species that migrate seasonally from one elevation to another. Altitudinal gradients also represent a more complete picture of the biota found in a given region.

One such altitudinal reserve was created on 13 April 1986 when Parque Nacional Braulio Carrillo, protecting approximately 31,401 ha of mid- to high-elevation forests on the upper slopes of Volcán Barva in Heredia Province, was increased by approximately 13,500 ha with the addition of a wildland area termed

Zona Protectora 'La Selva' and made part of the Cordillera Volcánica Central Forest Reserve (Fig. 1). Including the 1,500 ha of protected lowland forest of the adjacent privately operated La Selva Biological Station, there now exists a 60-km pro-

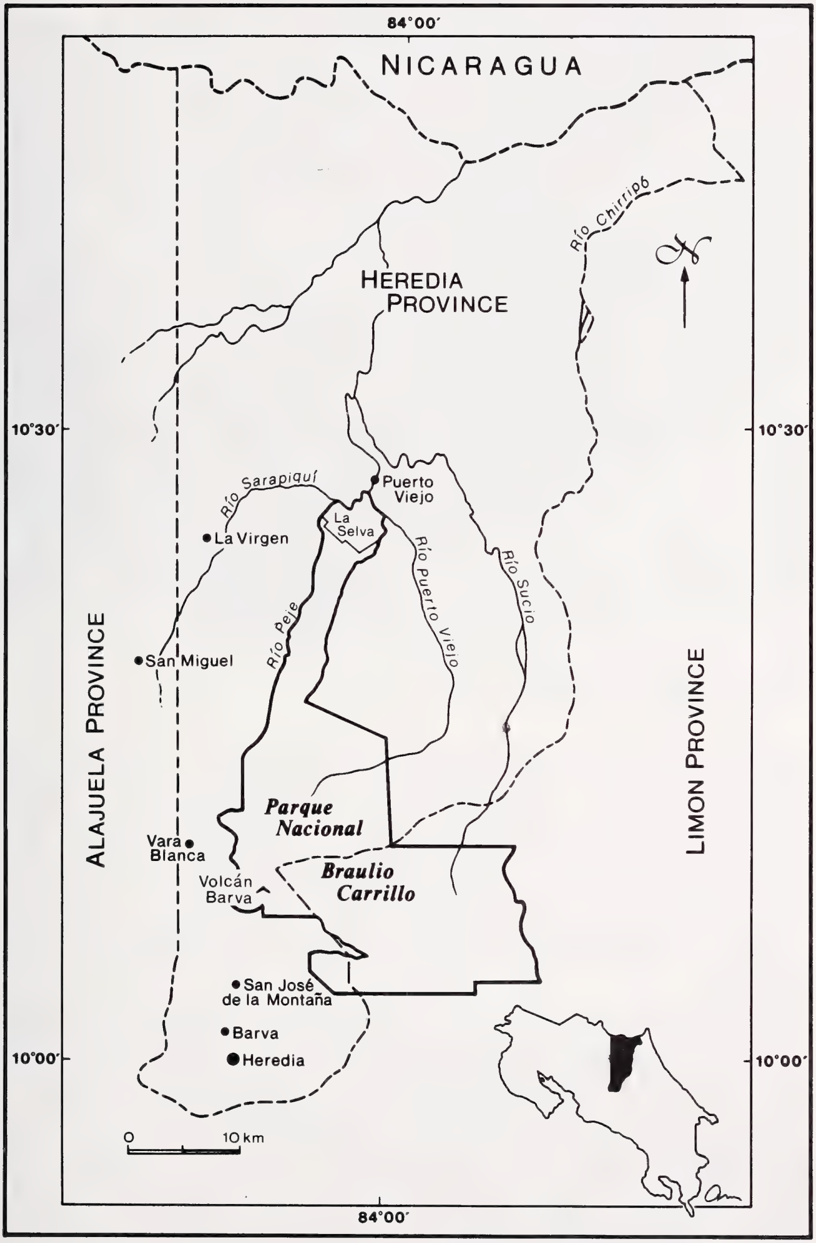


Fig. 1. Map of the study area.

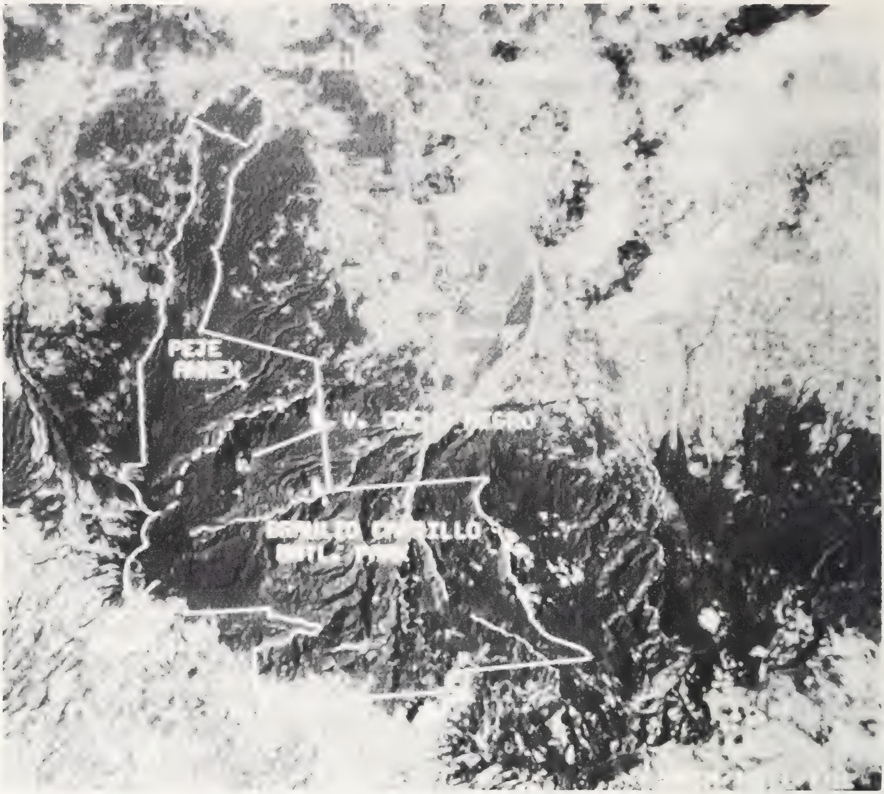


Fig. 2. Satellite photo of the study area. *Courtesy of Earth Resources Laboratory, National Space Technology Laboratory, NASA.*

tected corridor of forest from 30 m elevation at La Selva to 2,906 m at the top of Volcán Barva (Fig. 2). This corridor covers four life zones and two transitional zones between life zones, and is an important route for altitudinal migrants, including at least 35 species of birds. The expansion of Braulio Carrillo extends from the southwestern border of the La Selva Biological Reserve at 100 m and connects the Atlantic lowland forest around Puerto Viejo to the highlands of Volcán Barva. Together the biological reserve and national park contain 52,000 ha of uninterrupted forest.

Destruction of the rain forest in the Caribbean lowlands has proceeded at such an alarming rate that the two adjacent reserves, La Selva and Parque Nacional Braulio Carrillo, form a virtually isolated island of virgin forest (Fig. 3). The recent extension of the national park to La Selva, forming an elevational transect between the station and the higher elevations of Parque Nacional Braulio Carrillo, will be of vital importance in providing habitat to maintain breeding populations of the larger species with large home ranges that require extensive tracts of undisturbed habitat to maintain population levels, as well as

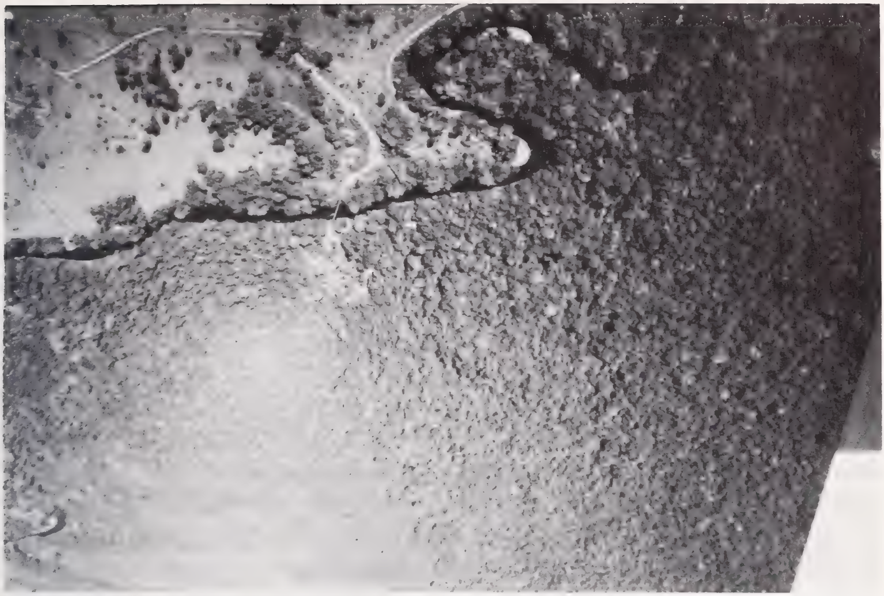


Fig. 3. Aerial photograph of La Selva Biological Station. Cleared area north of Río Puerto Viejo is outside the reserve. *Photo by G. S. Hartshorn.*

to ensure habitat availability on a seasonal basis for those species that are altitudinal migrants.

Along with Costa Rica's efforts in establishing national parks and wildlife refuges, the country has also afforded significant protection to its wildlife resources through recent enactment of rare and endangered species laws. The following 21 species are included in Costa Rica's listing of Rare and Endangered Species: water opossum (*Chironectes minimus*), Brazilian free-tailed bat (*Tadarida brasiliensis*), mantled howler monkey (*Alouatta palliata*), Geoffroy's spider monkey (*Ateles geoffroyi*), crested bare-face tamarin (*Saguinus oedipus*), squirrel monkey (*Saimiri oerstedii*), three-toed sloth (*Bradypus variegatus*), giant anteater (*Myrmecophaga tridactyla*), paca (*Agouti paca*), Harris' rice rat (*Oryzomys aphrastus*), mountain squirrel (*Syntheosciurus brochus*), southern river otter (*Lutra longicaudis*), mountain lion (*Felis concolor*), jaguar (*F. onca*), ocelot (*F. pardalis*), little spotted cat (*F. tigrina*), margay (*F. wiedii*), jaguarundi (*F. yagouaroundi*), Baird's tapir (*Tapirus bairdii*), white-lipped peccary (*Tayassu pecari*), and manatee (*Trichechus manatus*). Of these 21 species, at least 15 are, or were, found within the La Selva–Braulio Carrillo complex: water opossum, Brazilian free-tailed bat, mantled howler monkey, Geoffroy's spider monkey, three-toed sloth, giant anteater, paca, southern river otter, mountain lion, jaguar, ocelot, margay, jaguarundi, white-lipped peccary, and Baird's tapir.

The La Selva Biological Station supports a mammalian fauna comprising at least 114 species belonging to 9 orders. Included are 65 bats, 16 rodents, 14 carnivores, 6 edentates, 5 marsupials, 3 primates, 3 artiodactyls, 1 rabbit, and 1 perissodactyl. Although Braulio Carrillo is much more poorly known than La Selva, it is safe to assume that those species of mammals that have been recorded at La Selva are, or at least were, present in adjacent Braulio Carrillo. If we add to this list the species known to occur in the national park that are not present at La Selva, the fauna of Braulio Carrillo consists of at least 142 species, including 79 bats, 23 rodents, 15 carnivores, 7 marsupials, 6 edentates, 4 artiodactyls, 3 primates, 2 rabbits, 2 shrews, and 1 perissodactyl. This is undoubtedly a conservative estimate because we strongly suspect that additional field work will add to this list (see Species of Possible or Probable Occurrence in the Area). The greater species richness of bats than of all other species combined is not unusual for Neotropical faunas (Findley and Wilson 1983). There are 5 to 10 additional species of bats, a marsupial, and a few rodents that eventually may be found to occur at La Selva. Overhunting before protection of the area likely resulted in the extirpation of giant anteaters and white-lipped peccaries from La Selva. Tapirs, collared peccaries, pacas, agoutis, monkeys, and squirrels probably were reduced in numbers due to hunting pressure before the 1953 purchase of Finca La Selva by L. R. Holdridge. Numbers of these species, along with those of carnivores and rabbits, appear to be increasing in recent years, as protection of wildlife has been a high priority for the current owners, the Organization for Tropical Studies (OTS). Several species of bats and some of the marsupials may have benefited from human activities in the area. Today, the La Selva reserve–Parque Nacional Braulio Carrillo complex, with its elevational extension from near sea level to the top of Volcán Barva at more than 2,900 m, probably contains the best representation of a tropical mammalian fauna found anywhere in Central America (Timm, in press; Wilson, in press).

Most regions of Central America were visited early by educated European explorer–naturalists. These early scientists and dedicated amateurs played a vital, but now often overlooked, historical role in obtaining specimens from remote areas, depositing them in museums where they could be studied by scientists, and in recording observations on natural history and the abundance of organisms before habitat disturbance by expanding human populations. An outstanding example of these naturalists in Central America was the British mining engineer T. Belt, who recorded in great detail his 4 years spent in the Santo Domingo area of central Nicaragua (Belt 1874). He accurately described much of the animal and plant life of the region in addition to the geology. On the South American continent such explorers included Charles Darwin and Alexander von Humboldt.

The first formal collection of mammals from Costa Rica was made by W. M. Gabb during his study of the geography, geology, and paleontology of the lower Talamanca Mountains in 1874 and was sent to the U.S. National Museum of Natural History in Washington, DC. Gabb was employed by M. C. Keith, the builder of the Limón–San José railway, to survey the Talamanca region of Costa Rica for mineral deposits and for possible railway construction routes. Although he was unsuccessful in locating sufficient mineral deposits and a feasible railway construction route, he provided an excellent scientific account of the sparsely populated and rugged area, including a reliable report on the region's few remaining Indians, and he made a valuable zoological collection. Gabb's specimens included several new species of mammals, some of which subsequently were described by J. A. Allen. F. Du Cane Godman and O. Salvin produced a multi-volume *Biologia Centrali-Americana*, beginning in 1879, and one of the early volumes was devoted to mammals (Alston 1879–1882). Alston's book included a table listing the occurrence of each species of mammal in each central American country. His list included 66 species from Costa Rica.

The first checklist devoted strictly to Costa Rican mammals was compiled by the German physician A. von Frantzius (1881). In 1854, at the age of 33, he moved to Costa Rica to improve his health, and opened a drugstore in San José that became a center for local naturalists (Gómez and Savage 1983). He made the first significant collection of mammals from the Meseta Central (Central Valley), which he sent to specialists in Germany and the United States for identification and study. His checklist included 56 native species and many others of probable occurrence. Frantzius' assistant, J. C. Zeledón, who under his tutelage later developed an international reputation as an ornithologist, also collected many specimens of mammals that are deposited in the U.S. National Museum of Natural History. Zeledón made considerable contributions to the advancement of science in Costa Rica as a cofounder of the Museo Nacional, collaborator with foreign scientists, teacher, and book collector. The so-called ''drugstore gang'' included A. Alfaro, the first director of the Museo Nacional in San José, and G. K. Cherrie, a taxidermist who collected many specimens of mammals for that museum and others in the United States. Alfaro (1897) published a checklist of Costa Rican mammals that included 121 species.

The first mention in the literature of mammals from La Selva and the general vicinity was by Slud (1960:76) in *The Birds of Finca 'La Selva', Costa Rica*, his classic study of the avifauna. Concerning the mammals observed at La Selva during his year's study, he wrote ''A howler monkey may roar at any time of day and sometimes night. . . . Mammals, except agoutis, squirrels, tayras, and monkeys, are seldom to be observed. Of the big cats I saw only tracks.''

Students and faculty of the OTS courses have made significant contributions to our understanding of the mammalian fauna of La Selva, and indeed throughout Costa Rica. Shortly after Finca La Selva was purchased by OTS in 1968, we began netting bats there, assisted over the years by the many students in OTS courses. D. E. Wilson was a faculty member and R. K. LaVal was a student in the first course to visit La Selva in 1968. D. M. Armstrong was a student in the second course to visit in 1968 (Armstrong 1969). M. A. Mares visited there in 1969 as a student (Mares and Wilson 1971). Wilson continues to study bats there during OTS courses. LaVal spent several months there in 1973 and 1974 studying bats (LaVal 1977; LaVal and Fitch 1977). R. M. Timm first visited La Selva in 1974 as an OTS student (Foster and Timm 1976; Timm and Mortimer 1976), and has continued to work there and teach with OTS. C. S. Vaughan first visited La Selva in 1978 as an OTS student and has continued to work at the station and to bring students from his classes there.

T. H. Fleming studied the rodent fauna in 1970 and 1971. The number of small mammals, including marsupials, known from La Selva increased greatly during this period (Fleming 1973). At the same time, large mammals were observed more frequently as the number of trained observers increased.

During 1973 and 1974, LaVal sampled the bat fauna intensively using both mist nets and harp traps. His efforts dramatically increased the number of species known to occur at La Selva, several of which were new to the country (LaVal 1977; LaVal and Fitch 1977).

Information on all mammals has continued to accumulate with OTS's continued sponsorship of courses at the site and with the increased number of resident and visiting researchers. A log book is maintained to record mammal sightings, and considerable information has accumulated over the years. Likewise, our knowledge of the entire mammalian fauna of Costa Rica has increased tremendously since Goodwin's (1946) faunal study. Our estimate of the country's terrestrial mammalian fauna is more than 200 species. With 114 species, La Selva contains more than half the mammalian species known to occur in Costa Rica.

A 12-day scientific expedition to the Zona Protectora in 1983 made a preliminary evaluation of the resources there and estimated 800 species of trees and 400 species of birds. The expedition recorded 17 species of frogs and toads, 27 species of reptiles, and 18 species of mammals. Expedition members found 28 new plant species and 12 others not previously known from Costa Rica (Pringle et al. 1984).

With this information in hand, a more extensive expedition organized by the Organization for Tropical Studies began on 25 March 1986 and covered a transect from the La Selva Biological Station to the top of Volcán Barva (Fig. 1). The team of researchers included mammalogists, botanists, entomologists, herpetologists, invertebrate zoologists, and ornithologists, who studied various aspects of the biological richness and uniqueness of this area. This report covers only the mammal survey, the objectives of which were to determine general distributions and relative abundances of mammal species along the altitudinal transect between La Selva (30–137 m) and Volcán Barva (2,906 m).

We have not addressed the biogeographic affinities of this mammalian fauna since several recent reviews treat the biogeography of Costa Rican mammals from a variety of perspectives. Timm (in press) and Wilson (in press) treat the biogeographic relations of the mammalian fauna of La Selva, McPherson (1985, 1986) discusses the biogeography of Costa Rican rodents, and Savage (1974) provides an interesting review of the Isthmian Link and the evolution of Neotropical mammals.

Study Sites

Tropical wet forest on the Caribbean slopes of Costa Rica is found from sea level to about 150 m. Tropical wet forest cool-transition changes at 250 to 300 m to tropical premontane wet-transition rain forest, which is found from 300 to 500 m. Tropical premontane rain forest, from 500 to 1,500 m, lower montane rain forest, from 1,500 to 2,500 m, and montane rain forest, from 2,500 to 2,906 m, make up the other life zones found in Parque Nacional Braulio Carrillo.

The team of mammalogists on the 1986 expedition worked out of six camps situated at roughly 300 m, 700 m, 1,000 m, 1,500 m, 2,050 m, and 2,600 m (Fig. 1). We began at the 300-m site and spent 4–7 days at each site before moving up to the next camp. Censusing of larger mammals was done along the main trails at each study site by searching for animals and their signs (tracks, droppings, and so forth). Information was gathered from La Selva Biological Station (30–137 m) based on our previous knowledge of the site and the logbook of mammal sightings kept by staff, students, and researchers.

The first site (10°22′N, 84°03′W), which contained an abandoned farm and logging operation, was in a valley along the Río Cantarrana from 270 to 300 m, 11 km south and 4.5 km west of Puerto Viejo. The thick vegetation consisted of introduced weeds on the valley floor near the buildings; trees included *Cecropia*, *Ochroma lagopus*, and *Welfia georgii*. Primary and secondary forest was found about 200 to 300 m outside of the camp site and enclosed it on three sides. Mean annual rainfall for this area is estimated at 4,000 mm. Key tree species found in the forest at this elevation included *Minquartia guianensis* and *Pentaclethra macroloba*. Trap lines were placed along the main trail in primary forest, along streams, and in abandoned pasture; mist nets were placed in the first two environments.

The 700 m site was in pasture adjacent to the Río Cascante, 1 km south and 11.5 km east of San Miguel de Sarapiquí (10°18′N, 84°05′W). In abandoned pasture, we found shrubs and dense grass, and isolated individual trees that remained from earlier clearing. Primary forest was found adjacent to the camp site. Rainfall at this tropical premontane rain forest site could be as much as 4,500 mm/year. Key tree species found in the forest at this elevation include *Carapa guianensis* and *Terminalia amazonia*. Traps were set along the main trail in primary forest, along streams, and in pasture; mist nets were placed in the first two situations.

The third site was in primary forest at 1,000 m, 3.5 km south and 11.5 km east of San Miguel (10°17′N, 84°05′W) along the Río San Rafael. This site was surrounded by virgin tropical premontane rain forest. Both traps and mist nets were set along the trails and streams.

The 1,500-m site was located 9 km south and 11.5 km east of San Miguel (10°14′N, 84°05′W). It was in primary forest within the lower montane life zone. Key tree species at this elevation included *Ocotea austinii* and *Quercus corrugata*. The site was noticeably wetter, had a lower canopy, more saturated soils, and heavier moss growth than we found at the lower elevations. We set traps and mist nets along the main trail at the 1,000-m and 1,500-m sites.

The fifth study site (10°01′N, 84°07′W), at 2,050 m, was situated in an abandoned pasture 5 km east of Vara Blanca. Traps and mist nets were placed in the nearby primary forest along the main trail and along a small stream. Landslides seemed common at this elevation, probably caused by unstable soils, steep slopes, and high rainfall. Key tree species at this elevation again included *Ocotea austinii* and *Quercus corrugata*.

We used a guard station located 2 km north and 0.5 km east of Sacramento for camp at 2,600 m. It is on the Pacific side of Volcán Barva, and the nearby habitats are mostly pasture and several successional stages of forest. This site is within the montane rain forest life zone. Key tree species included *Drymys winterii* and *Quercus costaricensis*. Traps and mist nets were set along the road and in pastures found between forest patches.

The La Selva Biological Station is the field station of the Organization for Tropical Studies located 3 km south of Puerto Viejo de Sarapiquí (10°27′N, 84°00′W); elevation ranges from 35 to 135 m. Mean annual rainfall is 3,990 mm, with the wettest months being November, December, and February; mean monthly temperatures range from 24.5° C (December) to 26.1° C (April). La Selva lies within the tropical wet forest zone and grades into tropical premontane wet forest, with lowland evergreen forest the dominant forest type. Vegetation and habitat types of La Selva have been described by Slud (1960), Holdridge et al. (1971), Sawyer and Lindsey (1971), Hartshorn (1983), D. Lieberman et al. (1985), and M. Lieberman et al. (1985). One unusual feature of the subcanopy of the La Selva forest is the diversity and abundance of dwarf palms (Hartshorn 1983), especially the broad-leaved species, *Geonoma congesta* and *Asterogyne martiana*. The fruits and seeds of these palms serve as food for small mammals and the leaves are used by *Dermanura watsoni* for tent construction. The forest at La Selva is complex with perhaps as many as 400 species of trees; however, *Pentaclethra macroloba* (Mimosaceae) is the dominant tree species. Because of possible errors in identification by untrained observers, logbook notations from La Selva were screened by us. We have included only those reports that we believe to be reliable, unless otherwise discussed in the species accounts.

The habitat types along the La Selva–Volcán Barva altitudinal transect were described in greater detail by Hartshorn and Peralta (1988).

Specimen Data

Each species of mammal presently or historically recorded from Heredia Province, Costa Rica, as well as those possibly occurring there but whose presence is unverified by specimens, is treated separately in the accounts that follow. The basis of each species account is the natural history data obtained during this study, including distribution, relative abundance, reproductive characteristics, habitat use, parasites, food habits, and taxonomic comments as appropriate. All known records from the province and references to pertinent literature are included.

The colloquial or vernacular name(s) for each species is listed in English and then in Spanish immediately following the scientific name heading each species account. Spanish names listed herein are those used within this region of Costa Rica. Colloquial names for mammals often vary from country to country and even between different regions of the same country. Although there is little variation within Costa Rica in colloquial names for easily observed mammals, these are sometimes different than names used in neighboring countries. For example, in Costa Rica *tigrillo* refers to the gray fox (*Urocyon cinereoargenteus*), whereas in most Latin American countries *tigrillo* can refer to the margay (*Felis wiedii*). In Costa Rica, *zorro* refers to either of the two species of skunks that occur there, whereas in many Spanish speaking countries *zorro* refers to foxes. *Agouti paca* is a common game species throughout the tropics; in Costa Rica, and in adjacent Nicaragua, it is known as the *tepezcuintle*, but this name is not used everywhere in Latin America. The word is derived from the Indian name for the species. As nonmammalogists cannot distinguish most of the many species of bats, there are few local colloquial names in Spanish for bat species other than those that are direct translations of the English common name. Thus, we have not included Spanish names for most of the bats.

Standard external measurements (total length, length of tail vertebrae, length of hind foot, and height of ear from notch) were recorded in millimeters, weight was recorded in grams. On the basis of size and pelage characteristics, each animal was placed into one of three age classes: juvenile, subadult, or adult.

Specimens listed under ''Specimens examined'' were personally examined by one or more of us. The localities listed in both the ''Specimens examined'' and ''Additional records'' sections are reported as they were recorded by the original collector on specimen labels. Many specimens dating from the 1960's have distances recorded in miles and elevation in feet. Accordingly, we have kept the original English measures rather than convert these measures to metric equivalents. The one exception to maintaining the original locality data is that we have standardized the locality for specimens taken from La Selva. As the name for and formal status of this property have varied over the years, herein we use the name that has been most frequently associated with specimens in collections, ''Finca La Selva, 3 km S of Puerto Viejo.'' Specimens preserved from the 1986 Zona Protectora Expedition were divided between the Universidad Nacional de Costa Rica (a representation of the species collected), Field Museum of Natural History (primarily marsupials and rodents), and U.S. National Museum of Natural History (primarily bats). Specimens listed under ''Additional records'' either were taken from the literature or, for one reason or another, were not examined by one of us. In some cases, specimen identifications and localities were provided to us by curators of the collections in which they were housed, and we have not verified their identifications. The order for listing specimens is according to locality of capture as follows: alphabetical by reference point, then sequential north to south; those from the same latitude referenced to the same point are in order west to east. Sight records are so listed in the individual species accounts and we included these only when we were quite certain a correct identification was made. The arrangement of orders and families follows Hall (1981). Genera and species within a genus are treated in alphabetical order. Abbreviations designating specimens housed in museum collections are as follows:

AMNH	American Museum of Natural History, New York
CAL	California Academy of Sciences, San Francisco
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
KU	Museum of Natural History, University of Kansas, Lawrence
LACM	Natural History Museum of Los Angeles County, Los Angeles
LSUMZ	Louisiana State University Museum of Zoology, Louisiana State University, Baton Rouge
MNCR	Museo Nacional de Costa Rica, San José
MSB	Museum of Southwestern Biology, University of New Mexico, Albuquerque
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station
TTU	The Museum, Texas Tech University, Lubbock
UCR	Universidad de Costa Rica, San José
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
UNA	Universidad Nacional de Costa Rica, Heredia
USNM	United States National Museum of Natural History (including collections of the United States Biological Survey)

Accounts of Species

In the following accounts of mammals from the La Selva Biological Reserve–Parque Nacional Braulio Carrillo elevational transect, 142 species belonging to 10 orders and 32 families are included on the basis of documentation of their occurrence in Heredia Province. In addition, one species is considered as extirpated from the region, and comments are made concerning five species that may occur or have occurred in the past within the province, but whose presence there lacks adequate documentation.

Species of Verified Occurrence

ORDER MARSUPIALIA

Family Didelphidae

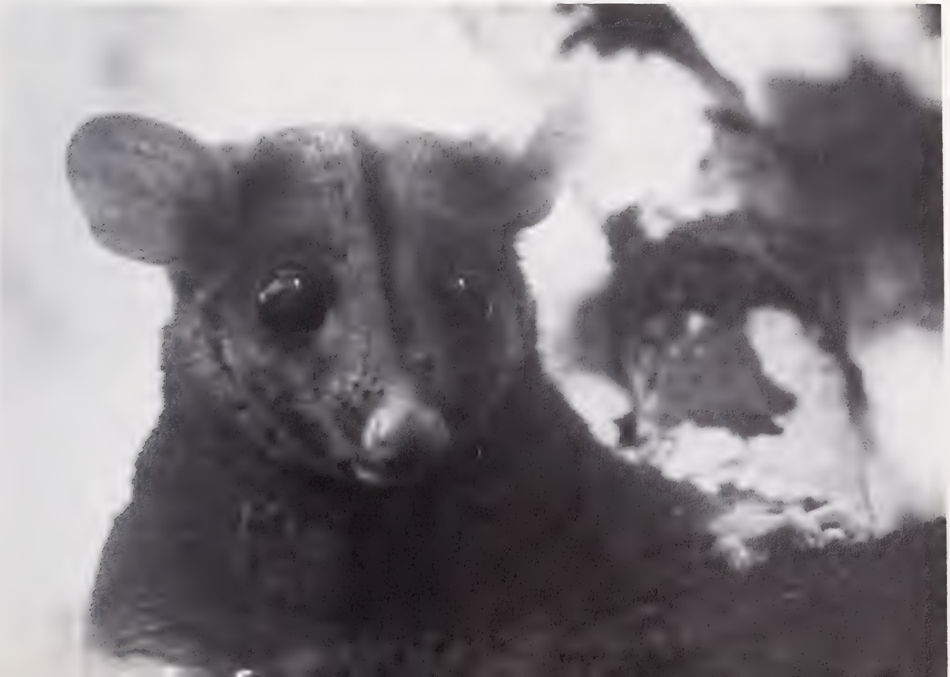
Caluromys derbianus
Woolly Opossum, Zorro de Balsa

Woolly opossums are found from southern Mexico south through western Colombia and extreme northwestern Ecuador (Fig. 4). Two subspecies of *Caluromys derbianus* are recognized in Costa Rica; *C. derbianus centralis* from the eastern slopes and lowlands and *C. derbianus pallidus* from the western slopes and lowlands. They are found from sea level to about 1,600 m. The biology of woolly opossums was reviewed by Bucher and Hoffmann (1980).

Woolly opossums have been observed at La Selva on at least 12 occasions. One was seen eating the fruits of *Piper* near the field station in July 1984. We examined an adult male woolly opossum (testes measured 11×9 mm) found dead on the Southwest Trail at La Selva on 25 March 1986. Another adult male was electrocuted on the wires behind the laboratory building on 20 January 1987.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, FMNH].

Fig. 4. Woolly opossum, *Caluromys derbianus*. *Photo by R. K. LaVal.*



Chironectes minimus
Water Opossum, Zorro de Agua

Water opossums are found from southern Mexico south through Central America to the Amazon and Orinoco river basins in South America (Fig. 5). One subspecies, *Chironectes minimus panamensis*, is found throughout the wet tropical lowlands of Costa Rica, although few specimens exist. Water opossums are found at least as high as 1,300 m in Costa Rica although their numbers and distribution have been reduced due to the degradation in quality of many streams. The biology of this species was reviewed by Marshall (1978).

One *C. minimus* was observed swimming in the Río Cantarrana near the 300-m base camp in April 1986, and another was seen in the same area in January 1983 (Pringle et al. 1984). Water opossums have been reported only seven times at La Selva between February 1979 and August 1988.

Specimen examined (1)—Puerto Viejo, Río Sarapiquí, 300 ft [1 male, UMMZ].

Didelphis marsupialis
Southern Opossum, Zorro Pelón or Zarigüeya

The southern opossum is widespread throughout the Central and South American lowlands (Fig. 6). In Costa Rica it is found country-wide except at higher elevations in the Cordillera Central and the Talamanca Mountains. In a revision of the *Didelphis* of Central and North America, Gardner (1973) recognized only a single subspecies of *D. marsupialis* from Mexico and Central America, *D. m. caucae*. Hall (1981), however, listed six subspecies of *D. marsupialis* from Central America, recognizing *D. m. richmondi* from extreme southeastern Nicaragua and northeastern Costa Rica in addition to *D. m. caucae* from the rest of the country. We concur with Gardner that *D. m. richmondi* is not a distinct subspecies, and that all *D. marsupialis* from Costa Rica should be considered *D. m. caucae*. The biology of *D. marsupialis* was reviewed by Gardner (1983a).

We saw opossums on numerous occasions at 200, 300, 680, and 750 m, although most often at 680 m. They are reported frequently near the La Selva Biological Station. In July 1974 we found an adult female opossum with five pouch young near the La Selva field station, on 3 July 1986 an adult female and four young were observed there, and on 8 July 1988 an adult female and two young were observed. Vaughan captured *D. marsupialis* at least 15 times at La Selva in live traps baited with chickens, meat, and fish and set for small wild felids in 1984–85. In this area, opossums are found in both forest and clearings. Pringle et al. (1984) reported *D. marsupialis* near their Cantarrana base camp in Parque Nacional Braulio Carrillo at 300 m in June of 1983.

External measurements for two adult males and one adult female we captured are as follows: total length, 790 mm, 840 mm, 818 mm; length of tail, 401 mm, 460 mm, 416 mm; length of hind foot, 67 mm, 65 mm, 67 mm; height of ear from notch, 54 mm, 55 mm, 55 mm. Testes on the two males measured 22×12 mm and 19×11 mm.

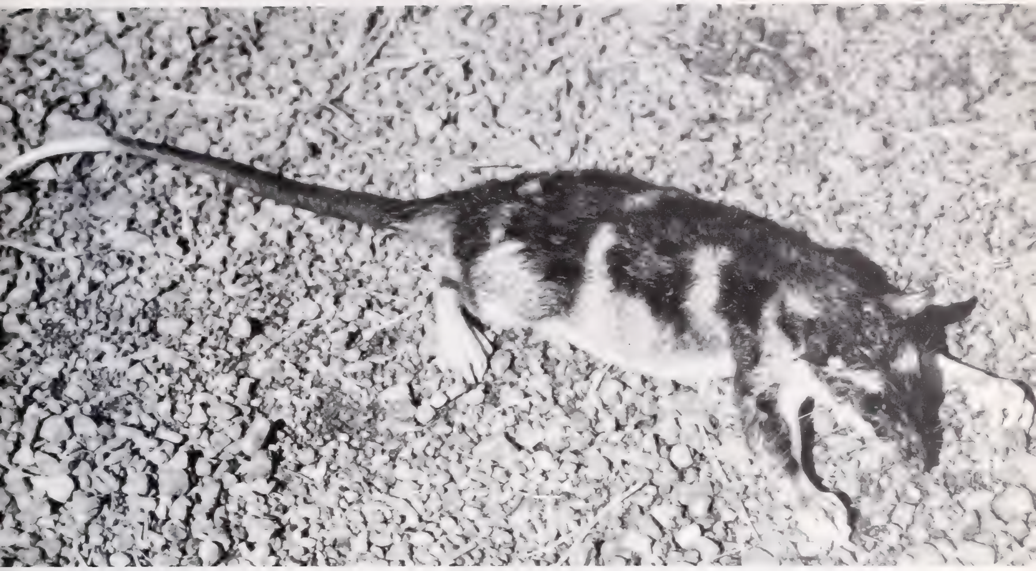
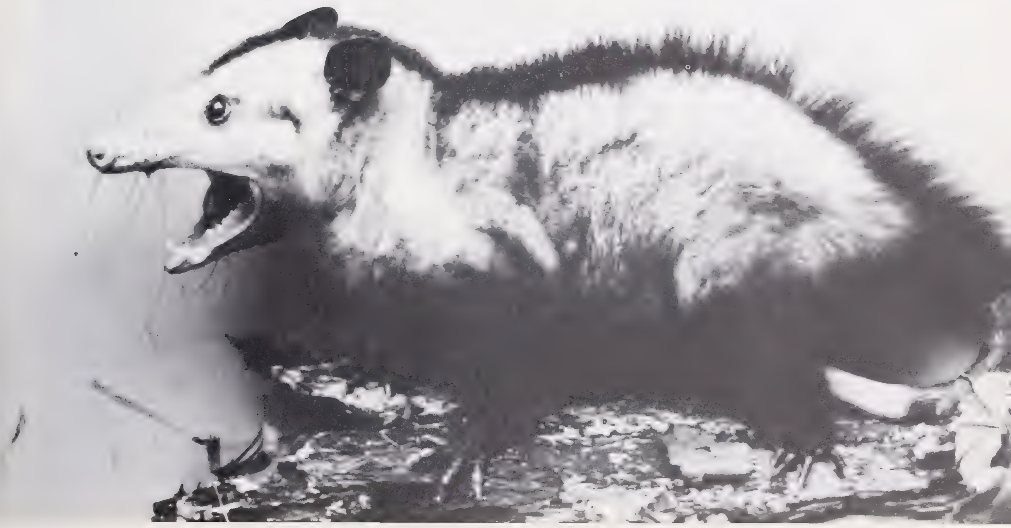


Fig. 5. Water opossum, *Chironectes minimus. Photo by R. W. McDiarmid.*

Ectoparasites found on *D. marsupialis* include two species of ticks, *Amblyomma* sp. (11 larvae, 3 nymphs) and *Ixodes luciae* (2 males). This represents the first record of *I. luciae*, a Neotropical opossum tick, from Costa Rica.

Specimens examined (3)—1 km S, 11.5 km E of San Miguel, 680 m [2 males, 1 female, FMNH].

Fig. 6. Southern opossum, *Didelphis marsupialis. Photo by A. L. Gardner.*



Marmosa alstoni
Alston's Opossum, Zorra or Zorricí

Alston's opossum, *Marmosa alstoni*, is found in the Caribbean lowlands and adjacent mountain slopes from Belize to southeastern Costa Rica and in Colombia (Fig. 7). *Marmosa alstoni* is considered by some to be a subspecies of the widely distributed South American species, *M. cinerea*. In Costa Rica, Alston's opossum ranges from sea level to about 1,600 m. Although little has been published about the biology or distribution of this species, it is relatively common in appropriate habitats. Vaughan had a group of *M. alstoni* living in his house near Concepción at 1,500 m, which is just outside of Parque Nacional Braulio Carrillo. There are no records of this species from La Selva or Braulio Carrillo, but we suspect that it occurs in the park.

Specimen examined (1)—1 km NW of Concepción de San Rafael, 1,500 m [1 sex?, UNA].

Marmosa mexicana
Mexican Mouse-opossum, Zorra or Zorricí

Mexican mouse-opossums are found from eastern and southern Mexico to western Panama (Fig. 8). The subspecies *Marmosa mexicana zeledoni* is found throughout Costa Rica.

Marmosa mexicana has been seen or taken at La Selva on several occasions, although there are no previously published records of this diminutive opossum from the region. The first specimen from La Selva was a male collected by Casebeer and Starrett in the early 1960's (LACM 24121). The second specimen is a subadult female collected by LaVal on 5 February 1974 (KU 134859). Collett captured a *M. mexicana* between the 3- and 4-year-old successional plots at La Selva in summer 1975, and Anderson caught another in a live trap baited with banana there in July 1983; both were released. We have found skulls and jaws of *M. mexicana* in regurgitated pellets of the spectacled owl (*Pulsatrix perspicillata*) at La Selva on several occasions. No other evidence of small mammals was found in these pellets, suggesting that mouse opossums compose a significant portion of the diet of spectacled owls there, at least during the rainy season (when the pellets were found). Although there are few records of Mexican mouse-opossums from La Selva, it is likely that they are more common there than the records indicate. They are nocturnal, arboreal, secretive, and seldom observed. Systematic trapping and study of remains found in owl pellets are a much better indicator of their presence and density than are sight observations.

We collected juvenile, subadult, and adult Mexican mouse-opossums in late March and early April in Parque Nacional Braulio Carrillo. Testes measurements of two adult males were 10×6 mm and 8×6 mm. A single nymph of *Ixodes venezuelensis* was collected on *M. mexicana* and represents the first record of this tick on the Mexican mouse-opossum.

Specimens examined (14)—Finca La Selva, 3 km S of Puerto Viejo [1 female, KU; 1 male, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, UNA], 325 m [6 males, 2 females, FMNH; 1 male, UNA], and 340 m [1 sex?, FMNH]; 1 km S, 11.5 km E of San Miguel, 710 m [1 male, FMNH].

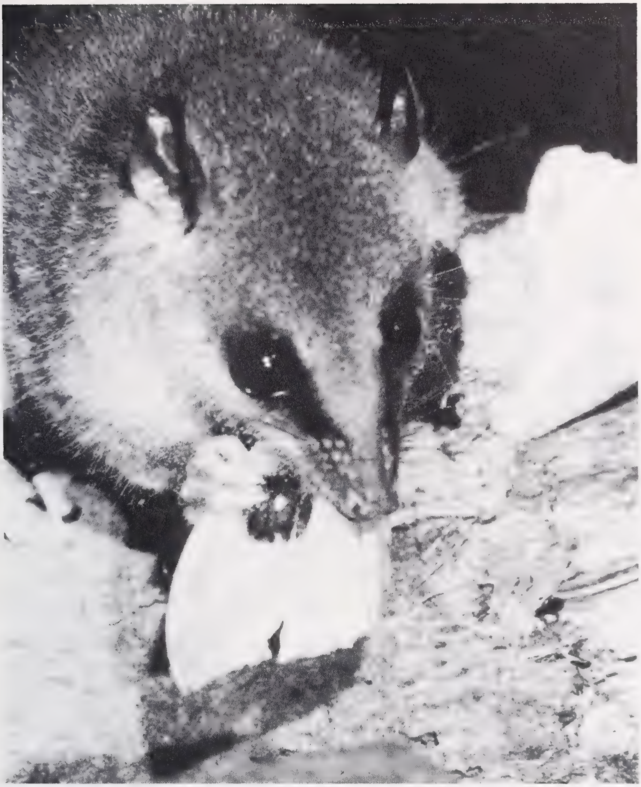
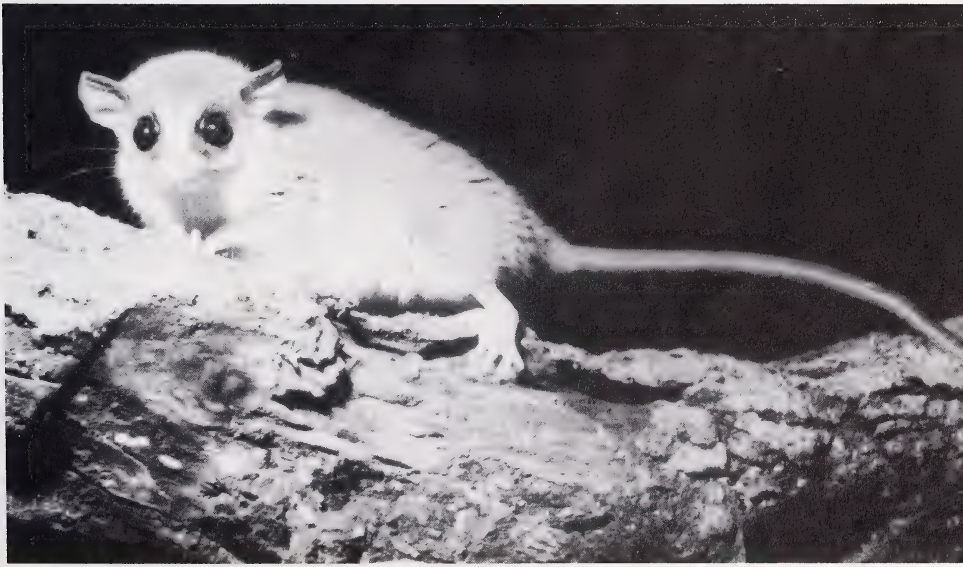


Fig. 7. Alston's opossum, *Marmosa alstoni. Photo by R. K. LaVal.*

Fig. 8. Mexican mouse-opossum, *Marmosa mexicana. Photo by B. L. Clauson.*



Metachirus nudicaudatus
Brown Four-eyed Opossum, Zorro de Cuatro Ojos

Brown four-eyed opossums are found from southeastern Nicaragua through much of South America to northern Argentina. Although Hall (1981) suggested that the range of brown four-eyed opossums included all of Costa Rica, until recently no specimens had been reported in the literature from Costa Rica. McPherson et al. (1985) noted that one specimen was collected at Angostura, near Turrialba in Cartago Province in 1876, and that for more than a century it went unrecognized as being the only specimen of *Metachirus nudicaudatus* from the country. They also reported a second specimen collected near Sarapiquí in Heredia Province in 1983. These specimens are from 600 m and 200 m, respectively, both from the Caribbean slopes.

Several individuals have recorded observations of animals they considered to be *M. nudicaudatus* at La Selva over the years. We believe that most, if not all of these observations were actually sightings of gray four-eyed opossums (*Philander opossum*). Although *M. nudicaudatus* and *P. opossum* are similar in size (*Metachirus* is slightly smaller) and appearance, they are not particularly closely related. The only field character useful in separating these two species is that *Metachirus*, as its common name implies, is various shades of brown, whereas *Philander*, as its common name implies, is various shades of gray. These two species are difficult to distinguish in the field, especially at night under poor light. The use of the name *M. nudicaudatus* for all four-eyed opossums at La Selva seems to be based on a 1960's handwritten list of the mammals occurring there, where the species is listed as the only four-eyed opposum of the region. It seems likely that subsequent observers applied this name to any four-eyed opossums they observed, even though *Philander* is actually more abundant and thus more likely to be observed. Given the apparent rarity of *M. nudicaudatus* in Costa Rica, it would be extremely valuable to have additional specimens of four-eyed opossums available for study.

Additional record (1)—Sarapiquí, Finca Cantarrana, near Río Peje, 200 m [1 male, MNCR—McPherson et al. 1985].

Philander opossum
Gray Four-eyed Opossum, Zorro de Cuatro Ojos

Gray four-eyed opossums are found from eastern Mexico south throughout Central America and much of tropical South America (Fig. 9). The subspecies *Philander opossum fuscogriseus* is found in Costa Rica from sea level to about 1,600 m.

On 14 April, an adult male *P. opossum* was captured crossing a fallen log near the Río Cascante at 680 m. External measurements for this male are: total length, 625 mm; length of tail, 310 mm; length of hind foot, 48 mm; height of ear from notch, 40 mm; weight, 605 g; testes measured 15×10 mm.

A fresh partial skull of a second adult *P. opossum* was found along the Río Cascante at 680 m; it appeared that the animal recently had been consumed

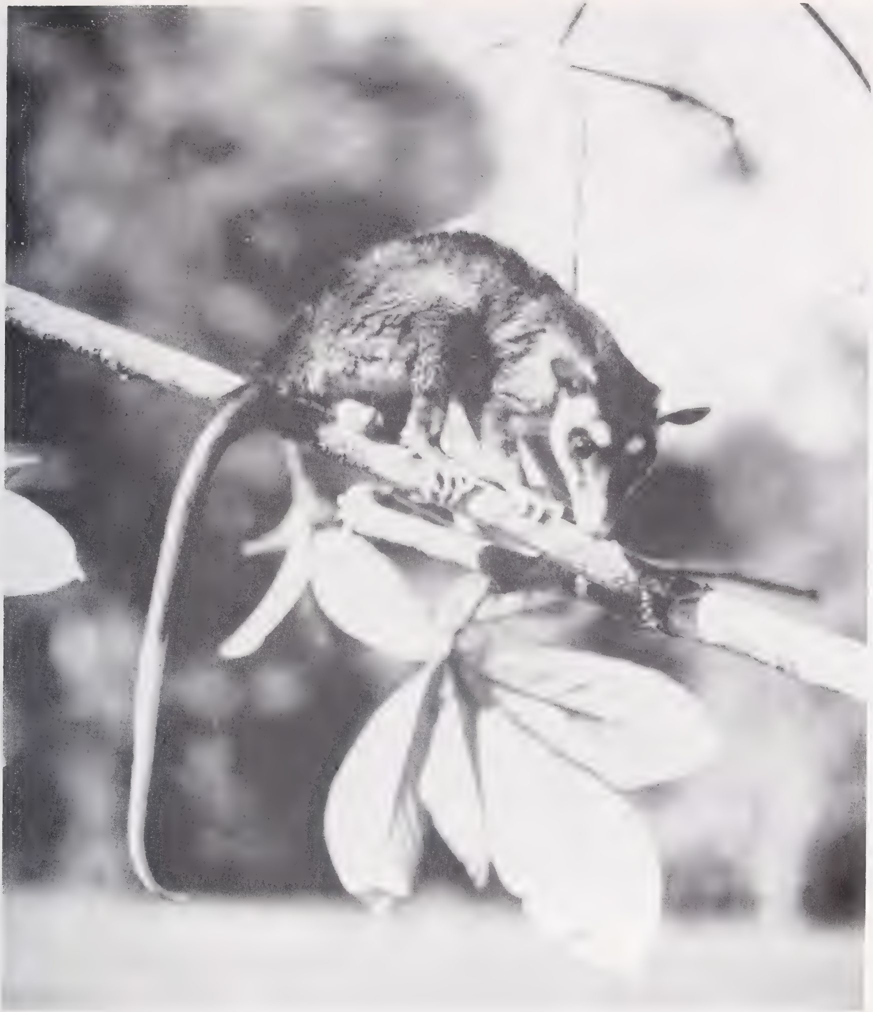


Fig. 9. Gray four-eyed opossum, *Philander opossum. Photo by B. L. Clauson.*

by a predator. On the evening of 30 March, a *P. opossum* was seen at 1.5 m height in a bush adjacent to the Río Cantarrana at 280 m. Four-eyed opossums were reported eight times near La Selva between February 1979 and April 1988 (see account of *Metachirus nudicaudatus*).

Ticks found on *P. opossum* include *Amblyomma* sp. (one nymph) and *Ixodes venezuelensis* (one nymph). *Ixodes venezuelensis*, a species in which males are unknown, is herein reported in Costa Rica for the first time based on this specimen and on our single specimen from *M. mexicana*.

Specimens examined (3)—Puerto Viejo, Río Sarapiquí, 300 ft [1 male, UMMZ]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, 1 sex?, FMNH].

ORDER INSECTIVORA

Family Soricidae

Cryptotis parva
Least Shrew, Musaraña

Least or small-eared shrews of the genus *Cryptotis* are widely distributed in eastern North, Central, and northern South America. The most widely distributed species, *C. parva*, is distributed in eastern North America from southern Canada through Mexico and Central America to the Chiriquí highlands of western Panama. Although there are only a few specimens of *Cryptotis parva* known from Heredia Province, we suspect that it is a common and abundant species on the western slope of Volcán Barva in the Meseta Central. A single subspecies of *C. parva*, *C. p. orophila* was recognized by Choate (1970) as occurring in Costa Rica.

The specimens from San José de la Montaña were captured in a home during the months of September through November. The specimens from San Miguel de la Montaña were taken by house cats in an area that included small fincas and houses, but little natural vegetation.

Specimens examined (6)—San José de la Montaña, ca. 1,800 m [1 male, 2 females, KU]; San Miguel de la Montaña, 1,690–1,700 m [1 male, 2 females, KU].

Cryptotis sp.
Least Shrew, Musaraña

A single, long-tailed *Cryptotis* was captured in a pasture above Alto del Roble northeast of Heredia, at 2,080 m by E. T. Hooper on 28 July 1968. He captured this adult male shrew in a snap-trap baited with peanut butter and set in a stump. It was originally identified as *C. gracilis*, and was reported as that species by Choate (1970) and Hall (1981). It clearly is related to that species; however, it may represent an undescribed taxon. This specimen currently is under study by N. Woodman and R. Timm.

Specimen examined (1)—Alto del Roble, 11 km NNE of Heredia, 2,080 m [1 male, UMMZ].

ORDER CHIROPTERA

Family Emballonuridae

Centronycteris maximiliani
Thomas' Bat

Thomas' bats are found from Veracruz, Mexico, south through Peru and Brazil (Fig. 10). The genus is monotypic (Husson 1978). Although Thomas (1912) described *Centronycteris centralis* as a distinct species, Sanborn (1937) concluded that it represented only the Central American subspecies of *C. maximiliani*. One subspecies, *C. m. centralis*, is found both in the Caribbean and Pacific wet tropical lowlands of Costa Rica, but there are few specimens on record.

Centronycteris maximiliani is uncommon throughout its range, and information on its natural history is almost nonexistent. The known distribution suggests

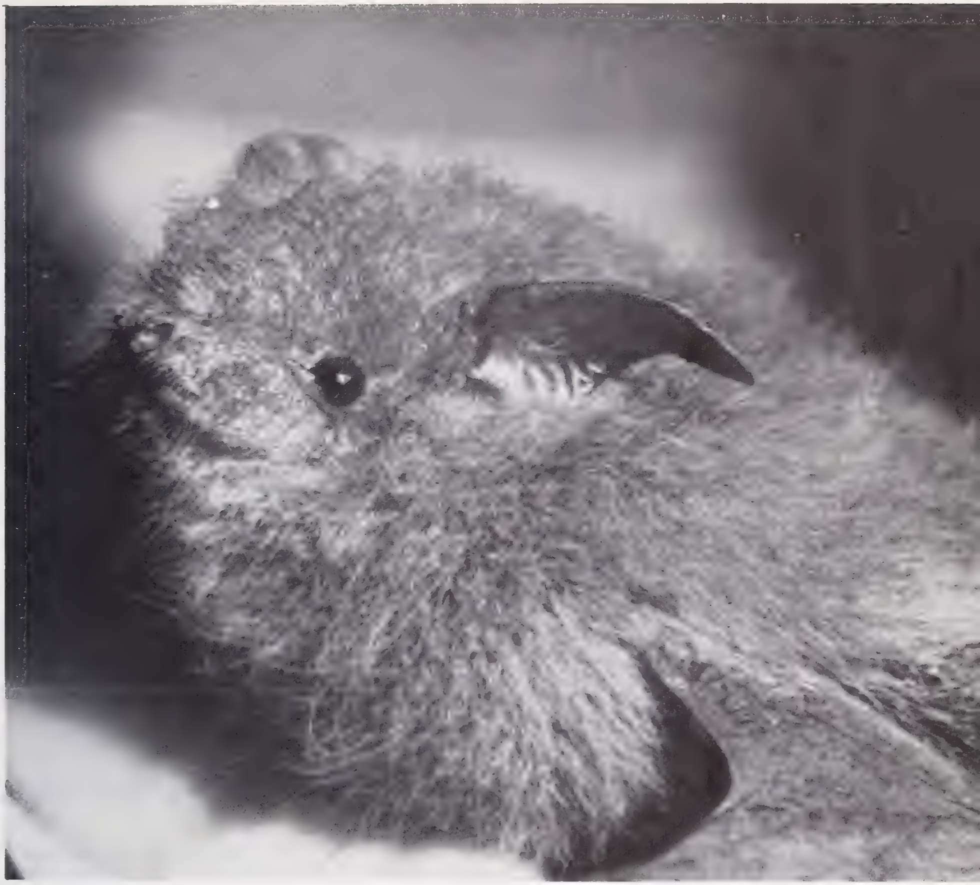


Fig. 10. Thomas' bat, *Centronycteris maximiliani*. *Photo by R. K. LaVal.*

that it is limited to lowland tropical rainforest. Both Goodwin (1946) and Albuja (1983) reported Ecuadoran specimens taken from tree holes. Although no data have been reported, *C. maximiliani* is almost surely insectivorous (Wilson 1973a). LaVal (1977) found pregnant females in May and subadults in September at La Selva, suggesting the monestrous pattern common to other emballonurids (Wilson 1973b).

The first Costa Rican specimen of *C. maximiliani* came from La Bijagua, on the Caribbean slope of Volcán Miravalles in Alajuela Province (Allen and Barbour 1923). Additional specimens were collected on the Osa Peninsula (Gardner et al. 1970; Starrett and Casebeer 1968). LaVal (1977) captured four individuals at La Selva in 1973. LaVal also observed a single individual roosting 12 m up on a tree trunk at Carrara Biological Reserve, in tropical moist forest on the Pacific slope.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, KU].

Cormura brevirostris
Wagner's Sac-winged Bat

Wagner's sac-winged bats are found from Nicaragua south through Central America to the Amazon basin in South America (Fig. 11). This monotypic species is the only member of the genus.

The biology of this uncommon emballonurid is poorly known. It is known to roost in hollow trees in South America (Sanborn 1941; Tuttle 1970). Fleming et al. (1972) reported insects from the stomachs of Panamanian *Cormura*. They also reported pregnant females only in April and May, suggesting a monestrous reproductive cycle.

Although rare at La Selva, we caught individuals occasionally in the second growth of the successional plots. Our only specimen from Parque Nacional Braulio Carrillo was taken in a mist net over the Río Cantarrana near the 300-m base camp. It is the only specimen record of this species for northern and eastern Costa Rica.

Specimen examined (1)—11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, USNM].

Cyttarops alecto
Short-eared Bat

The short-eared bat is known only from eastern Nicaragua, Costa Rica, Guyana, and Amazonian Brazil. The genus contains only this monotypic species. All specimens of *Cyttarops alecto* have come from tropical lowland rain forest. Natural history information on this rare species is limited to that provided by Starrett (1972). All Costa Rican specimens have been taken from roosts under palm leaves. This species is presumably insectivorous, like other emballonurids. Nothing is known of the reproductive cycle.

This rare species was known only by the type specimen from Brazil and a single specimen from Guyana (Thomas 1913) until 1964 when three individuals were reported from Los Diamantes, about 25 km east of Parque Nacional Braulio Carrillo (Starrett and de la Torre 1964). Starrett and Casebeer (1968) reported eight specimens from Puerto Viejo, 3 km north of La Selva. We did not encounter this species at higher elevations.

Specimens examined (5)—Puerto Viejo de Sarapiquí [1 male, 4 females, LACM].

Peropteryx kappleri
Greater Doglike Bat

Greater doglike bats are found from Veracruz, Mexico, south throughout Central America and much of tropical South America to southern Brazil (Fig. 12). The nominate subspecies, *Peropteryx kappleri kappleri*, is found throughout the range except for the type locality of the other named subspecies (*P. k. intermedia*) in Peru.

Individuals have been taken from sea level up to 1,500 m and in a variety of habitats. They roost singly or in small groups of mixed sex in shallow caves,

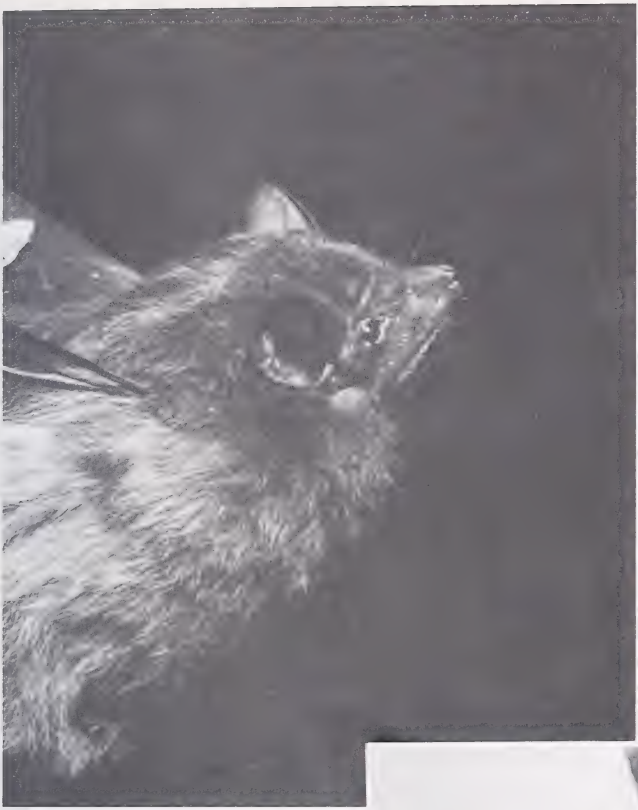


Fig. 11. Wagner's sac-winged bat, *Cormura brevirostris. Photo by B. L. Clauson.*

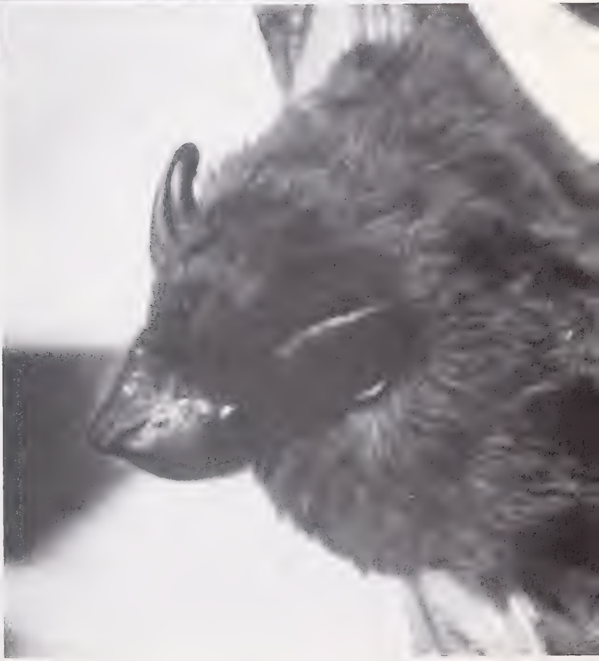


Fig. 12. Greater doglike bat, *Peropteryx kappleri. Photo by R. K. LaVal.*

rock crevices, and hollow trees (Bradbury and Vehrencamp 1976). This species is insectivorous. The breeding cycle is monestrous and highly synchronous (Rasweiler 1982).

LaVal (1977) frequently found these bats roosting on the undersides of fallen logs, which were supported above ground by buttresses. In several cases they were roosting stacked atop one another, as many as four deep. They are rarely captured in mist nests. We did not encounter this species in Parque Nacional Braulio Carrillo.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, MSB].

Rhynchonycteris naso
Brazilian Long-nosed Bat

Brazilian long-nosed bats are found from Oaxaca and Veracruz, Mexico, through Central America to central Brazil (Fig. 13). The genus contains only this monotypic species.

This is a lowland species commonly found along watercourses in both wet and dry tropical forests. Individuals roost in open situations, frequently on the undersides of tree trunks or logs extending out over watercourses. The species is insectivorous. Reproduction may be asynchronous or aseasonal and individual females may produce more than one young per year (Bradbury and Vehrencamp 1977).

Originally reported from Costa Rica on the basis of 10 specimens collected by G. K. Cherrie from an unknown locality (Allen 1897), this species first was reported from La Selva by Starrett and Casebeer (1968). An adult female with a near-term fetus 22 mm long was taken at La Selva on 18 July 1974. During the early 1980's, a colony of *Rhynchonycteris naso* was observed on numerous occasions roosting under the eaves of the old field station building. A group also roosted under the cement steps leading to the boat dock. In late July and early August of 1983, the colony contained 16 individuals; 2 of the females were suckling young.

Specimens examined (7)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [3 males, 2 females, MSB]; 4 mi W of Puerto Viejo de Sarapiquí, 92 m [1 male, TCWC]; 7.2 km W of Puerto Viejo, 100 m [1 male, KU].

Saccopteryx bilineata
Greater White-lined Bat

The greater white-lined bat is widespread from Colima, Mexico, to Brazil (Fig. 14). The two subspecies recognized by Alvarez (1968) are *Saccopteryx bilineata centralis* from Nicaragua northward, and the nominate race, *S. b. bilineata*, throughout Costa Rica and southward.

This insectivorous species occurs in a variety of habitats, generally limited to lowlands. Bradbury and Vehrencamp (1976) and Bradbury (1983a) provided considerable natural history information on *S. bilineata* in Costa Rica and at La Selva in particular. Roosting sites include inside hollow trees, between buttresses of large trees, and, occasionally, the sides of manmade structures. Reproduction is seasonally synchronized, and females are monestrous.

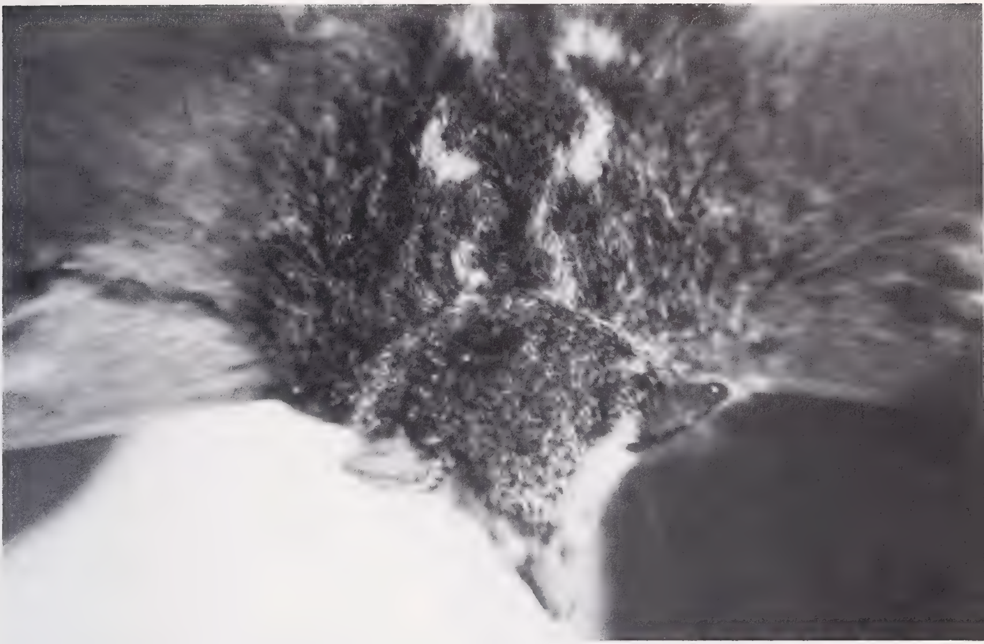


Fig. 13. Brazilian long-nosed bat, *Rhynchonycteris naso. Photo by D. E. Wilson.*

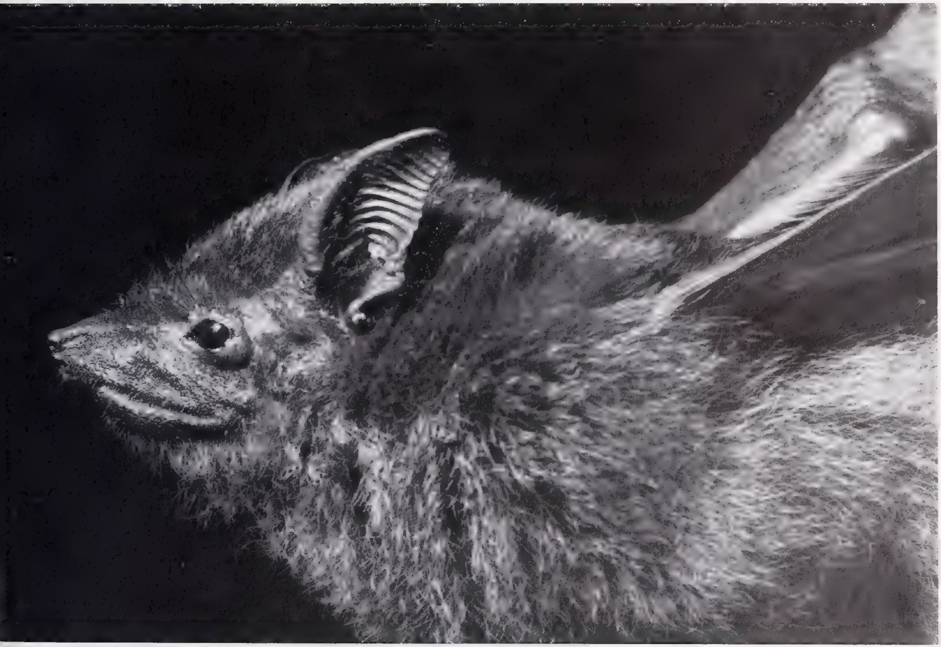


Fig. 14. Greater white-lined bat, *Saccopteryx bilineata. Photo by B. L. Clauson.*

Abundant throughout lowland Costa Rica, *S. bilineata* occurs at La Selva both in large colonies in hollow trees, and in smaller groups on the sides of buildings and in buttresses of large forest trees. On 1 August 1983 at La Selva, three harems of *Saccopteryx* were located by A. Alberts in a large ''Ceiba.'' One harem contained eight females, three with young; one contained five females, three with young; and one contained four females, one with young. Males seemed to spend most of their time at the territorial boundaries (A. Alberts, in litt.).

Specimens examined (13)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 male, 1 female, LACM; 5 females, MSB]; Puerto Viejo, Río Sarapiquí, 100 m [1 male, 1 female, KU; 2 females, UMMZ]; 2.5 km SE of Puerto Viejo [1 female, TCWC].

Saccopteryx leptura
Lesser White-lined Bat

Lesser white-lined bats are found from Chiapas, Mexico, south through Central America to eastern Brazil (Fig. 15). The species is monotypic.

Population dynamics were studied extensively in Costa Rica by Bradbury and Vehrencamp (1976). This species is less common than *Saccopteryx bilineata* in most areas, and seems to prefer more open roosting sites. Group size is also much smaller, but food habits and reproductive patterns seem similar.

Although previously known from Panama and Nicaragua, this species was first reported from Costa Rica by Starrett and Casebeer (1968). LaVal and Fitch (1977) reported seven individuals from La Selva. We did not encounter this species in Parque Nacional Braulio Carrillo.

Specimen examined (1)—Puerto Viejo, Río Sarapiquí, 300 ft [1 female, UMMZ].

Family Noctilionidae

Noctilio albiventris
Lesser Bulldog Bat

Lesser bulldog bats are found from Chiapas, Mexico, to Argentina (Fig. 16). The Costa Rican subspecies, *Noctilio albiventris minor*, is found throughout Central America to northern South America.

Primarily an inhabitant of wet tropical forests, this species forages for insects mainly over rivers, streams, and wetlands. Although roosts are known from hollow trees and caves, large colonies frequently are found in buildings. The reproductive cycle appears to be one of seasonal monestry (Hood and Pitocchelli 1983).

Apparently the first published record of *N. albiventris* from Costa Rica was that of Davis et al. (1964), who reported a single female from La Selva. LaVal and Fitch (1977) also reported capturing only a single individual, a pregnant female, in August. These bats, however, are common in the area and can be seen foraging over the Río Puerto Viejo, where we have netted them on several occasions, the most recent of which was in January 1987.

Specimen examined (1)—Puerto Viejo, Río Sarapiquí, 300 ft [1 male, UMMZ].

Additional record (1)—4 mi W of Puerto Viejo, 300 ft [1 female, TCWC].

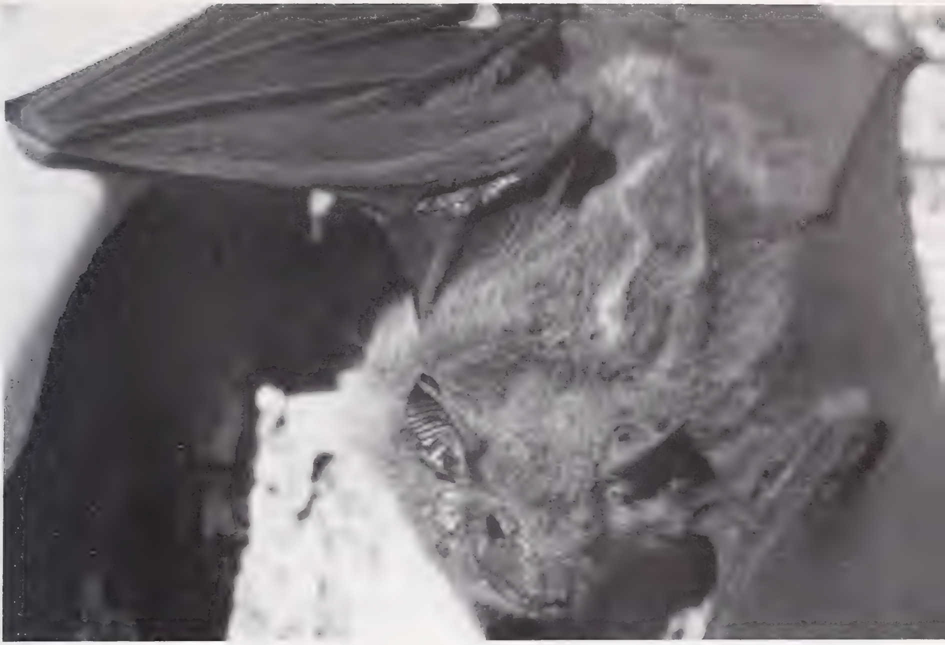


Fig. 15. Lesser white-lined bat, *Saccopteryx leptura. Photo by R. K. LaVal.*

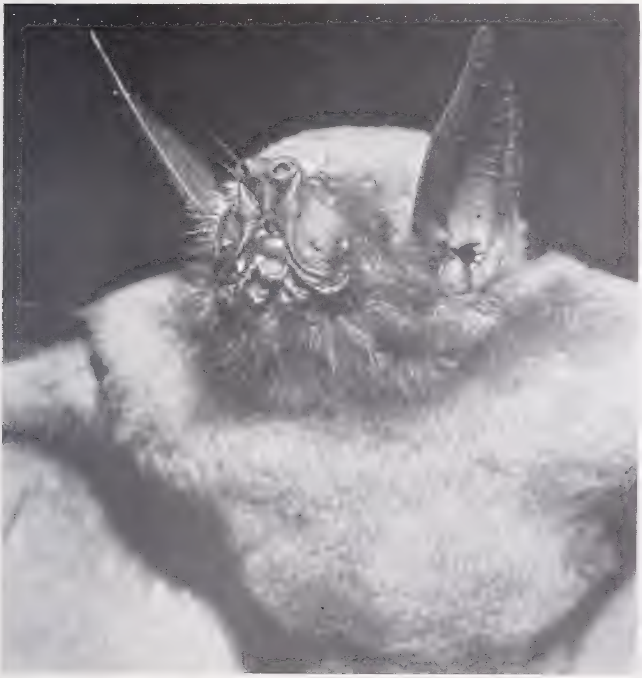


Fig. 16. Lesser bulldog bat, *Noctilio albiventris. Photo by B. L. Clauson.*

Noctilio leporinus
Greater Bulldog Bat

Greater bulldog bats are known from Sinaloa and Veracruz, Mexico, to Argentina (Fig. 17). The Costa Rican subspecies, *Noctilio leporinus mastivus*, is found throughout Central America and northern South America.

Although known from both dry and wet tropical forests, this species is found mainly along major lowland river systems. Roosts are known from hollow trees and sea caves (Hood and Jones 1984), and Mares et al. (1981) reported a night roost under a bridge occupied by several hundred individuals. These bats feed on insects and on fish, which they gaff at the surface of the water with their long claws (Brandon 1983).

The first record for Costa Rica was that of Carter et al. (1966). Although no specimens have been preserved from La Selva, these large bats can be seen foraging low over the Río Puerto Viejo. A group roosted under the cement steps leading to the boat dock in the late 1970's and early 1980's, but they have not used this site in recent years.

Specimens examined (2)—7.3 mi SE of Puerto Viejo [2 males, TTU].

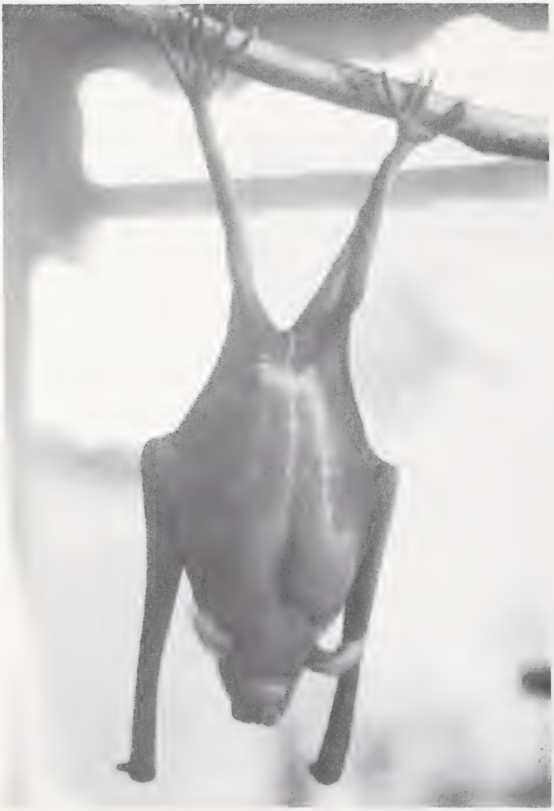


Fig. 17. Greater bulldog bat, *Noctilio leporinus. Photo by R. K. LaVal.*

Family Mormoopidae

Pteronotus davyi

Davy's Naked-backed Bat

Davy's naked-backed bats are found from central Sonora and southern Tamaulipas, Mexico, through Central America to northern South America (Fig. 18). The distribution of *Pteronotus davyi* in southern Central America and northern South America is poorly understood; this species is represented from Costa Rica, Venezuela, and eastern Peru by only a few specimens. There are apparently no records of Davy's naked-backed bat from Panama, Colombia, or Ecuador. In a recent revision of the family, Smith (1979) recognized three subspecies of *P. davyi*, and considered the nominate race *P. d. davyi* to be the subspecies found in Costa Rica. The biology and distribution of this species recently was reviewed by Adams (1989).

Starrett and Casebeer (1968) reported the first specimens of Davy's naked-backed bats from Costa Rica. They obtained a total of four specimens from three localities in northwestern Costa Rica; one of the localities was in Alajuela Province and two were in Guanacaste Province. On the basis of this report, Wilson (1983) listed the species as present at Palo Verde. There have been no other reports of this diminutive naked-backed bat from the country.

On 28 July 1983, J. Wenzel captured a single adult female in a mist net set in the arboretum clearing at La Selva. This is the first record of this species from the Caribbean lowlands of Costa Rica.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, KU].

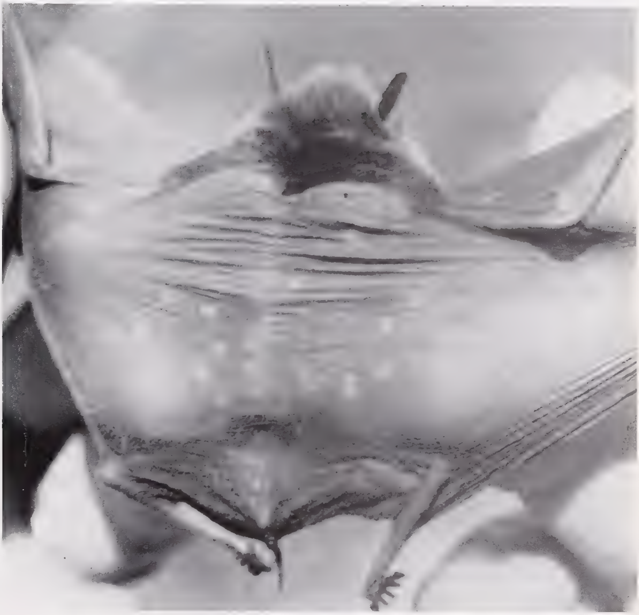


Fig. 18. Davy's naked-backed bat, *Pteronotus davyi. Photo by R. K. LaVal.*

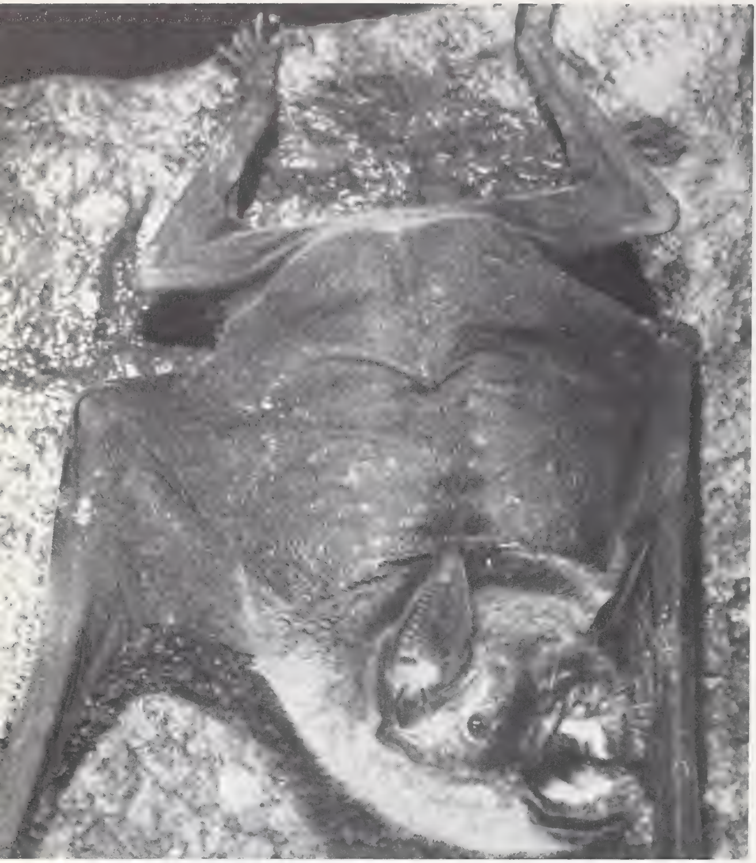


Fig. 19. Big naked-backed bat, *Pteronotus gymnonotus*. *Photo by R. K. LaVal.*

Pteronotus gymnonotus
Big Naked-backed Bat

Big naked-backed bats are widely distributed from Veracruz, Mexico, to southwestern Brazil (Fig. 19). The species is monotypic.

Although known from a variety of habitats, this species is primarily an inhabitant of lowland forests. Roosts are usually in caves, and colonies may be quite large. *Pteronotus gymnonotus* is an aerial insectivore. Reproduction has not been studied, but other members of the family are monestrous (Wilson 1973b).

The first Costa Rican record of this species was from Boruca (Sanborn 1932). Starrett and Casebeer (1968) shot individuals foraging above roadways in two localities in southern Costa Rica. Our specimen is the first record for the La Selva region. It was taken in a mist net set over the Río Cascante in an area where the forest had been cleared for pasture.

Specimen examined (1)—1 km S, 11.5 km E of San Miguel, 680 m [1 female, USNM].

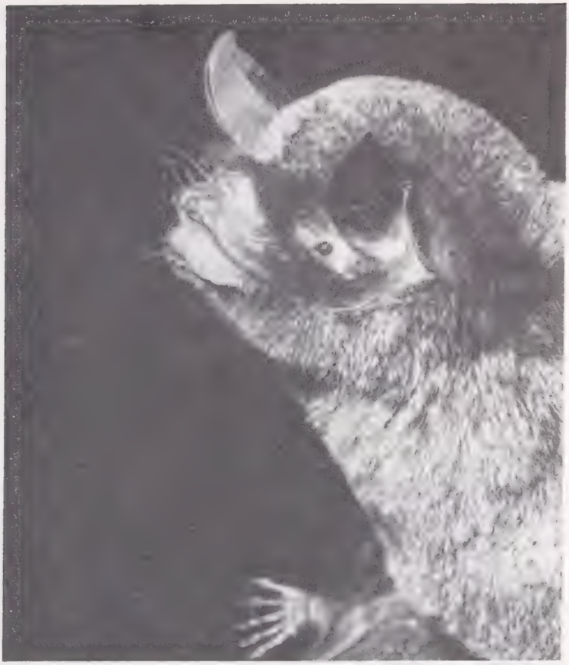


Fig. 20. Parnell's mustached bat, *Pteronotus parnellii. Photo by B. L. Clauson.*

Pteronotus parnellii
Parnell's Mustached Bat

Parnell's mustached bats are found from Sonora, Mexico, to Brazil (Fig. 20). This species is known from a broad range of habitats from sea level up to 3,000 m (Smith 1972). Two subspecies are known from Costa Rica: *Pteronotus parnellii mesoamericanus* from the Pacific side and *P. p. rubiginosus* from the Caribbean versant. Large colonies roost in caves and in mines (Herd 1983). Insects, which are the main food source, are captured on the wing. The reproductive pattern is one of seasonal monestry (Wilson 1973b).

Parnell's mustached bats are common throughout Costa Rica, and can be captured in mist nets set almost anywhere in the forest. They were netted regularly over the years in the primary forest at La Selva, although never in large numbers, and we found them to be common at lower elevations in Parque Nacional Braulio Carrillo. LaVal and Fitch (1977) captured 25 at La Selva; pregnant females were found from January through May.

Ectoparasites collected from *Pteronotus parnellii* include the bat flies *Nycterophilia parnelli* (5 males, 1 female), *Trichobius sparsus* (10 males, 6 females), and *Trichobius yunkeri* (15 males, 8 females).

Specimens examined (20)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, KU; 1 male, 1 female, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [3 females, USNM; 1 female, UNA]; 1 km S, 11.5 km E of San Miguel, 680 m [10 males, 1 female, USNM; 1 male, 1 female, UNA].

Family Phyllostomidae

Subfamily Phyllostominae

Chrotopterus auritus
Peter's False Vampire Bat

Peter's false vampire bats are found from the southern Mexican States of Oaxaca and Veracruz through Central America to the Guianas, across northern and southern Brazil, eastern Peru, and southeast to northern Argentina (Fig. 21). Although *Chrotopterus auritus* is widely distributed, there are few actual specimens of this species and we know little of its distribution and biology. *Chrotopterus auritus* probably is best considered as a monotypic species.

The diet of these large phyllostomines consists of small vertebrates and large insects. Medellín (1988) found that 86% of prey items from a roost in Mexico were vertebrates, and that 79% of those were rodents and shrews. Roost sites include hollow trees (Medellín 1988) and caves (Graham 1988). Wilson (1979) summarized what little information is available on reproduction in this species, and suggested that it is likely the young are born during the early part of the rainy season.

Little is known concerning the status of Peter's false vampire in Costa Rica. Goodwin (1946) listed *C. auritus* as a species occurring in Costa Rica; however, he did not cite either specimens from the country or localities, so it seems that he had no actual records available but included it because of suspected distribution. Starrett and Casebeer (1968) were the first to report specimens of *C. auritus* from Costa Rica. They obtained a total of seven males and one female from a single hollow log at Finca La Lola in Limón Province at 50 m elevation in July 1961 and September 1962. Wilson (1983) listed Peter's false vampire bat from Guanacaste Province.

On 8 May 1988, A. P. Brooke captured a single young adult female *C. auritus* at La Selva. The bat was mist-netted in primary forest at 1645 h; it was followed by radiotelemetry and released (A. P. Brooke, in litt.). This is the first record of Peter's false vampire bat from La Selva. Brooke (1988) found this female to direct foraging attacks only at birds and bats when they flew by, ignoring insects. She suggested that *C. auritus* has a ''sit-and-wait'' foraging strategy, hunting only selected, active prey.

Lonchorhina aurita
Tomes' Long-eared Bat

Tomes' long-eared bat is found from Oaxaca, Mexico, to Brazil (Fig. 22). Although Anthony (1923) named *Lonchorhina occidentalis* as a distinct species, recent workers have placed it in synonymy with *L. aurita*, which is considered monotypic (Lassieur and Wilson 1989).

Although mainly a bat of the primary forest, it has been taken in agricultural areas as well (Handley 1976). The most common roosting sites are caves or tunnels. Although this species is insectivorous and probably a foliage gleaner, Fleming et al. (1972) reported a single individual with fruit pulp in its stomach. The scant evidence available suggests a reproductive cycle tied to the rainy season.

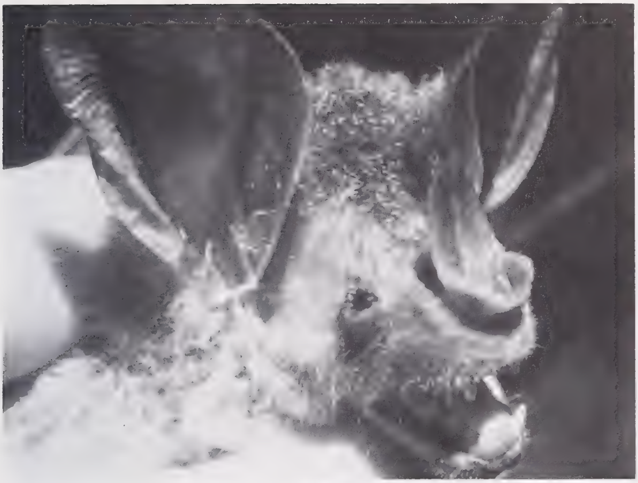


Fig. 21. Peter's false vampire bat, *Chrotopterus auritus. Photo by R. K. LaVal.*

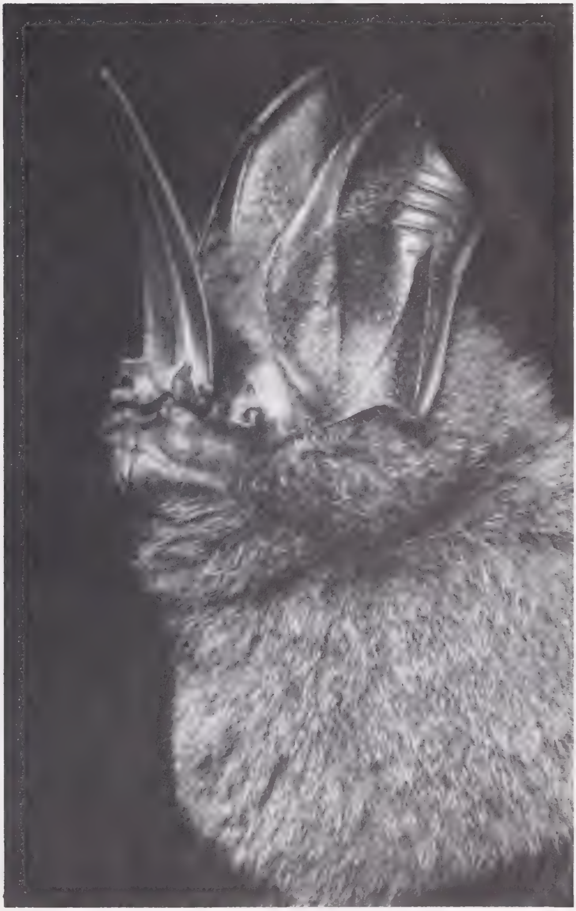


Fig. 22. Tomes' long-eared bat, *Lonchorhina aurita. Photo by B. L. Clauson.*

The first record of this species for Costa Rica is that of Nelson (1965), who collected 13 from a cave near Moravia de Turrialba in Cartago Province. This species has not been collected at La Selva. Our specimens from Parque Nacional Braulio Carrillo were mist-netted in primary forest. *Lonchorhina aurita* appears at mid-elevations in Braulio Carrillo, but is found at lower elevations elsewhere in its range.

Parasites collected from *L. aurita* include the bat flies *Speiseria ambigua* (1 male) and *Trichobius flagellatus* (12 males, 7 females).

Specimens examined (8)—11 km S, 4.5 km W of Puerto Viejo, 270 m [3 males, USNM]; 1 km S, 11.5 km E of San Miguel, 680 m [4 males, USNM; 1 male, UNA].

Macrophyllum macrophyllum
Long-legged Bat

Long-legged bats occur from Chiapas and Tabasco, Mexico, through Central America and South America to Argentina (Fig. 23). *Macrophyllum macrophyllum* is monotypic.

This species normally is captured over streams in forested habitats (Tuttle 1970). It is known to roost in caves and road culverts (Greenhall and Paradiso 1968) but probably also uses hollow trees. Gardner (1977) reported water striders (Gerridae) in the diet, and suggested that *Macrophyllum* might be the only completely insectivorous member of the subfamily Phyllostcminae. LaVal's (1977) data suggest that young are born in June or July, but little is known of the overall reproductive cycle (Wilson 1979). The biology of this species was summarized by Harrison (1975).

The species first was reported from Costa Rica by Starrett and Casebeer (1968) from Guanacaste and Limón Provinces. LaVal and Fitch (1977) reported capturing three at La Selva. One species of bat fly, *Trichobius macrophylli* (7 males, 2 females), was obtained on these long-legged bats at La Selva.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo [1 male, MSB]; 7.3 mi SE of Puerto Viejo [1 female, TTU].

Micronycteris brachyotis
Dobson's Large-eared Bat

Dobson's large-eared bat, a monotypic species, is found from Oaxaca and Veracruz, Mexico, to Amazonian Brazil. Although normally associated with forested habitats, this bat was reported roosting in savannahs by Husson (1978). Roost sites include caves, mines, and hollow trees (Medellín et al. 1985). Goodwin and Greenhall (1961) reported insects and fruit from stomachs of specimens from Trinidad. In Panama, Bonaccorso (1979) found evidence of a bimodal reproductive pattern.

The first Costa Rican specimens were taken by Fleming et al. (1972) in Guanacaste in 1970. LaVal and Fitch (1977) reported capturing three from La Selva. Apparently no specimens from the Caribbean lowlands have been preserved in collections.

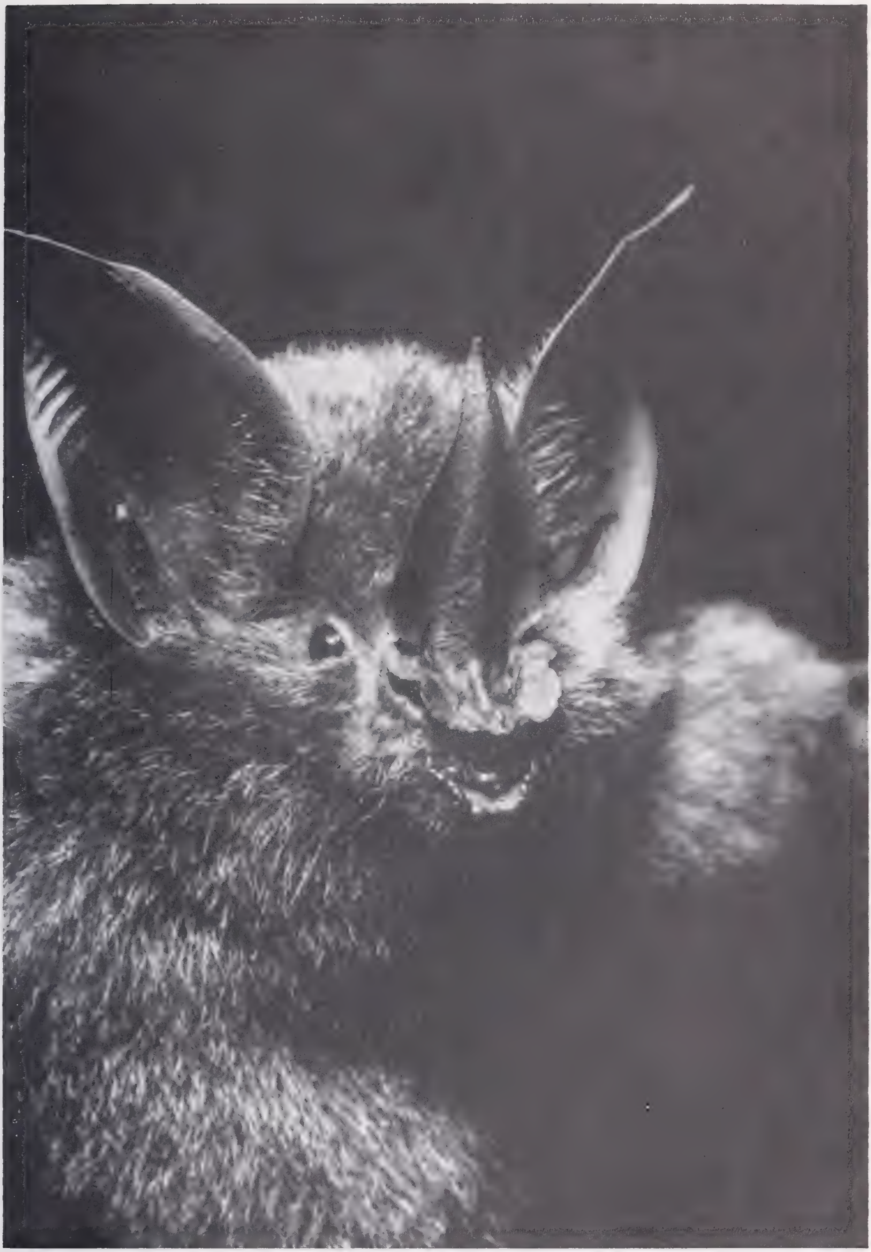


Fig. 23. Long-legged bat, *Macrophyllum macrophyllum. Photo by B. L. Clauson.*

Micronycteris daviesi
Davies' Large-eared Bat

Davies' large-eared bats are known from scattered localities ranging from Honduras to Peru and Amazonian Brazil. This monotypic species is sometimes placed in the separate genus *Barticonycteris*.

Little is known about the natural history of *Micronycteris daviesi*. Specimens have been caught in mist nets in mature forest (Hill 1964). Tuttle (1970) reported three individuals in a hollow tree roost in Peru. No information is available on food habits or reproductive pattern.

This species is known from Costa Rica only by specimens collected at La Selva by us in the early 1970's (LaVal 1977), and by a single adult we netted and released there at 1930 h on 26 March 1986. A bat fly, *Trichobius yunkeri* (one female) was obtained from *M. daviesi* at La Selva.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 male, MSB].

Micronycteris hirsuta
Hairy Large-eared Bat

Hairy large-eared bats occur from southern Honduras to Amazonian Brazil (Fig. 24). This monotypic species is most often collected in forested habitats, although Handley (1976) reported it in yards as well. These bats are known to roost in hollow trees, under bridges, in buildings, and in other manmade structures (Goodwin and Greenhall 1961). Wilson (1971) reported this species to be primarily insectivorous, but it consumes a variety of fruits during the dry season. There are some data suggesting the usual phyllostomid bimodal reproductive pattern (Wilson 1979).

Goodwin (1946) listed two specimens from Palmar and two specimens from Pozo Azul, and tentatively designated the latter as the type locality. Gardner et al. (1970) added a fifth specimen from Rincón de Osa on the Osa Peninsula. LaVal and Fitch (1977) reported four individuals from La Selva.

Specimens examined (3)—2.5 km SE of Puerto Viejo [1 male, CM]; Finca La Selva, 3 km S of Puerto Viejo [2 females, MSB].

Micronycteris megalotis
Brazilian Large-eared Bat

Brazilian large-eared bats occur from Tamaulipas and Jalisco, Mexico, to southern Brazil (Fig. 25). In Costa Rica, two subspecies are recognized: *Micronycteris megalotis mexicana* from the Pacific side and *M. m. microtis* from the Caribbean lowlands. This arrangement is based on few specimens (Gardner et al. 1970), and a study of geographic variation in this species would be useful.

This species uses a variety of habitats and occurs across a wide elevational range (Gardner et al. 1970). Many roosting sites, some of them unusual, have been reported for this species (Handley 1976): caves, mines, hollow trees, logs, stumps, buildings, bridges, wells, culverts, under roots, under rocks, and in large mam-

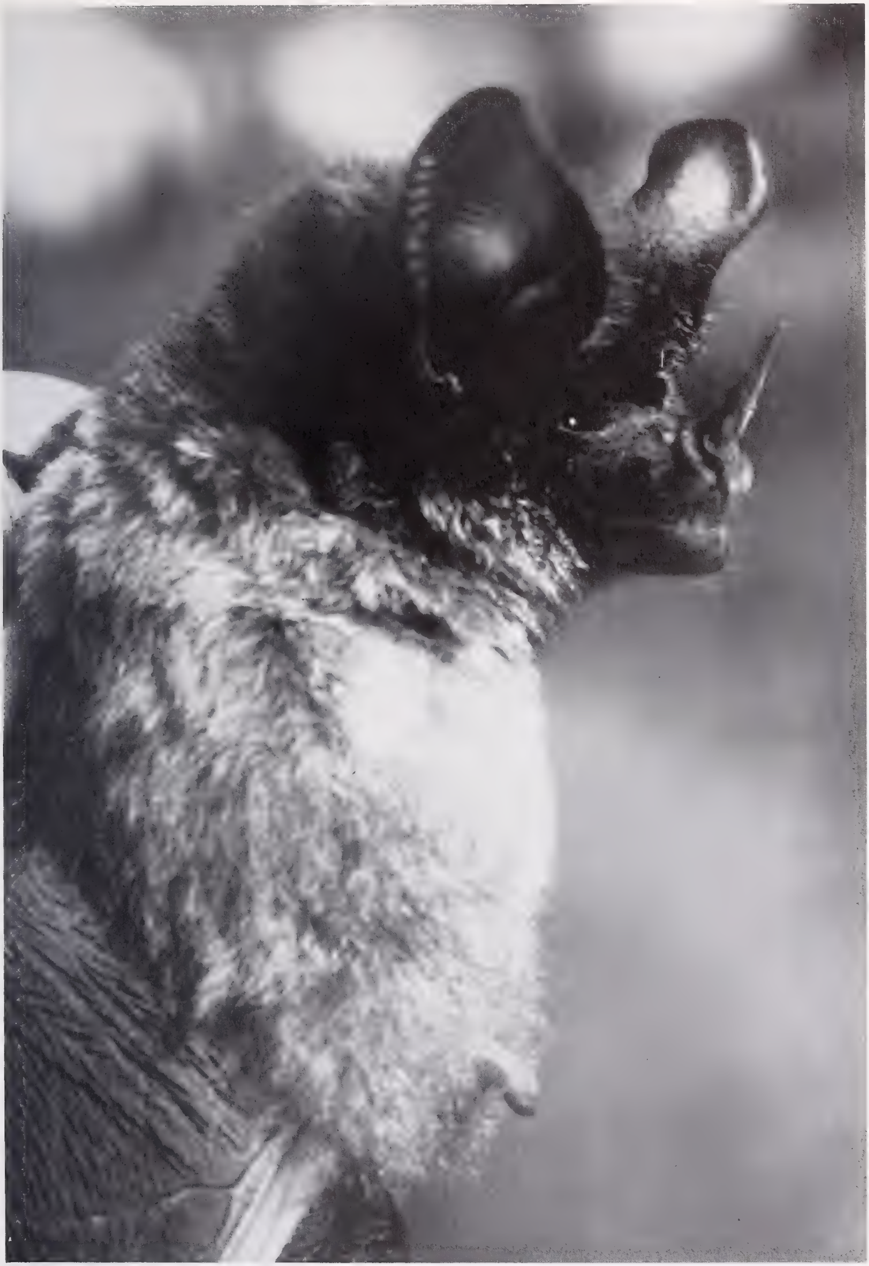


Fig. 24. Hairy large-eared bat, *Micronycteris hirsuta. Photo by R. K. LaVal.*

mal burrows. It feeds on fruit and insects, as do most phyllostomines. LaVal and LaVal (1980) found remains of insects representing several orders at night-feeding roosts of these bats at La Selva. There is no complete study of the reproductive cycle from a single locality.

Goodwin (1946) reported *M. m. microtis* from Río Sixaola and Gardner et al. (1970) recorded the first *M. m. mexicana* from the country. LaVal and Fitch (1977)

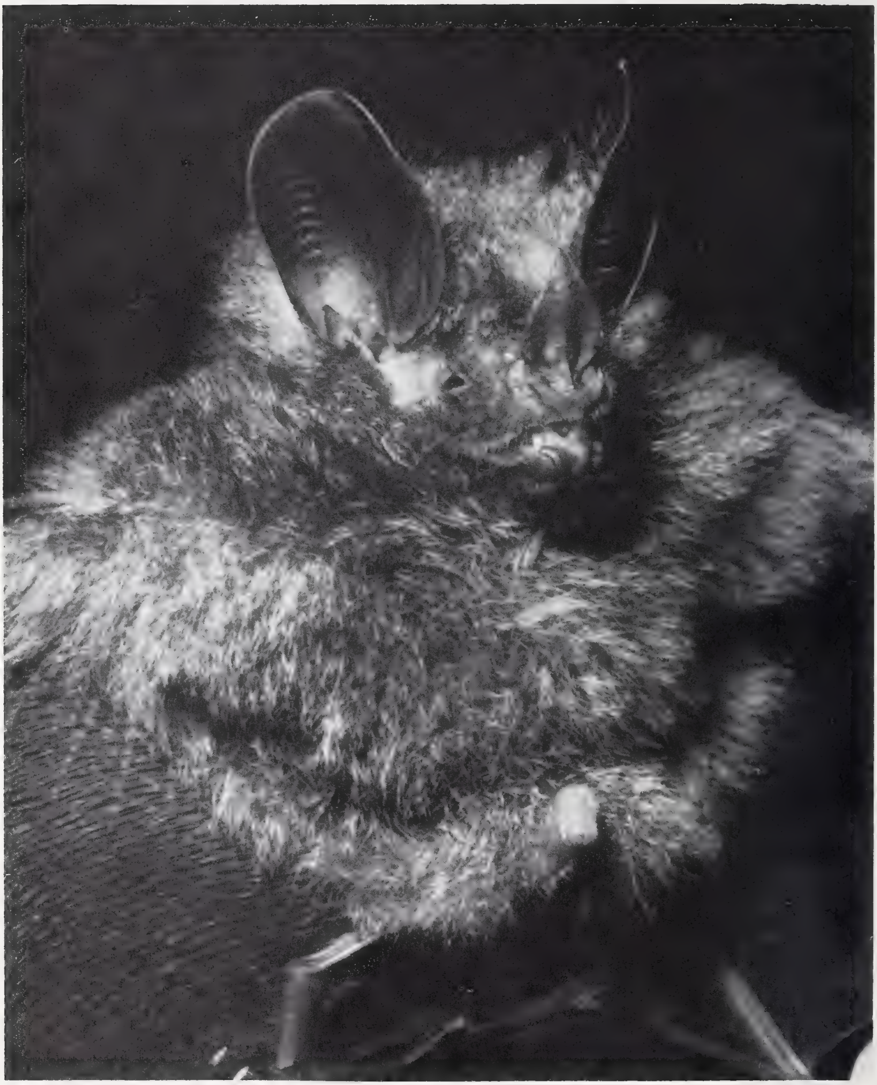


Fig. 25. Brazilian large-eared bat, *Micronycteris megalotis. Photo by B. L. Clauson.*

captured 21 specimens at La Selva. One individual was netted over a small stream in primary forest.

Specimens examined (9)—Puerto Viejo, Río Sarapiquí, 300 ft [2 males, 1 female, UMMZ]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 male, LACM; 1 male, 1 female, MSB]; 5.7 mi S of Puerto Viejo [1 female, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, USNM].

Micronycteris minuta
Gervais' Large-eared Bat

Gervais' large-eared bat, a monotypic species, is known from Nicaragua to southern Brazil (Fig. 26). It is primarily an inhabitant of forested regions, but specimens also are known from agricultural areas (Williams and Genoways 1980). Roosts have been reported in hollow trees, caves, and mines (Sanborn 1949). These bats feed on insects and plant material (Fleming et al. 1972). Reproduction occurs at the beginning of the rainy season, but the complete cycle is unknown (Wilson 1979).

The first Costa Rican records were reported by Gardner et al. (1970) from Cartago, Guanacaste, and San José Provinces. LaVal and Fitch (1977) reported one from La Selva. We caught and released a second individual at La Selva in 1973. Apparently no individuals of *Micronycteris minuta* from La Selva have been preserved.

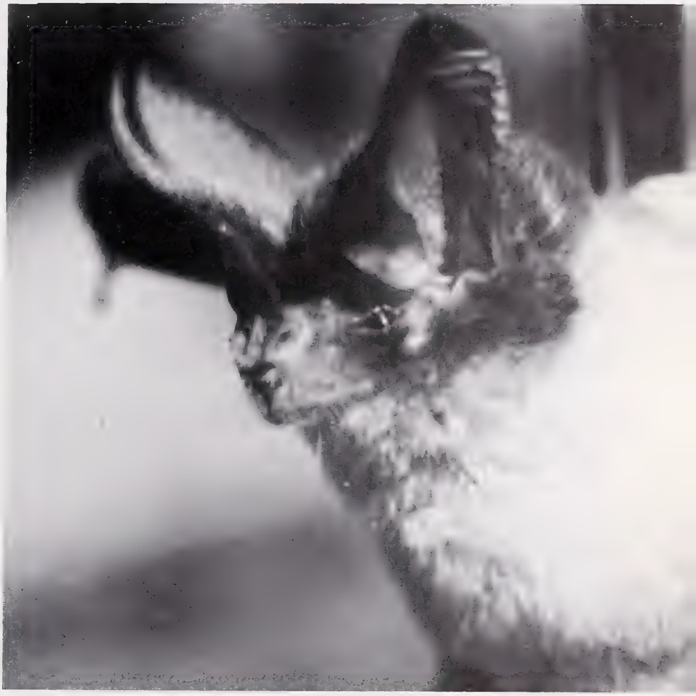


Fig. 26. Gervais' large-eared bat, *Micronycteris minuta. Photo by R. K. LaVal.*

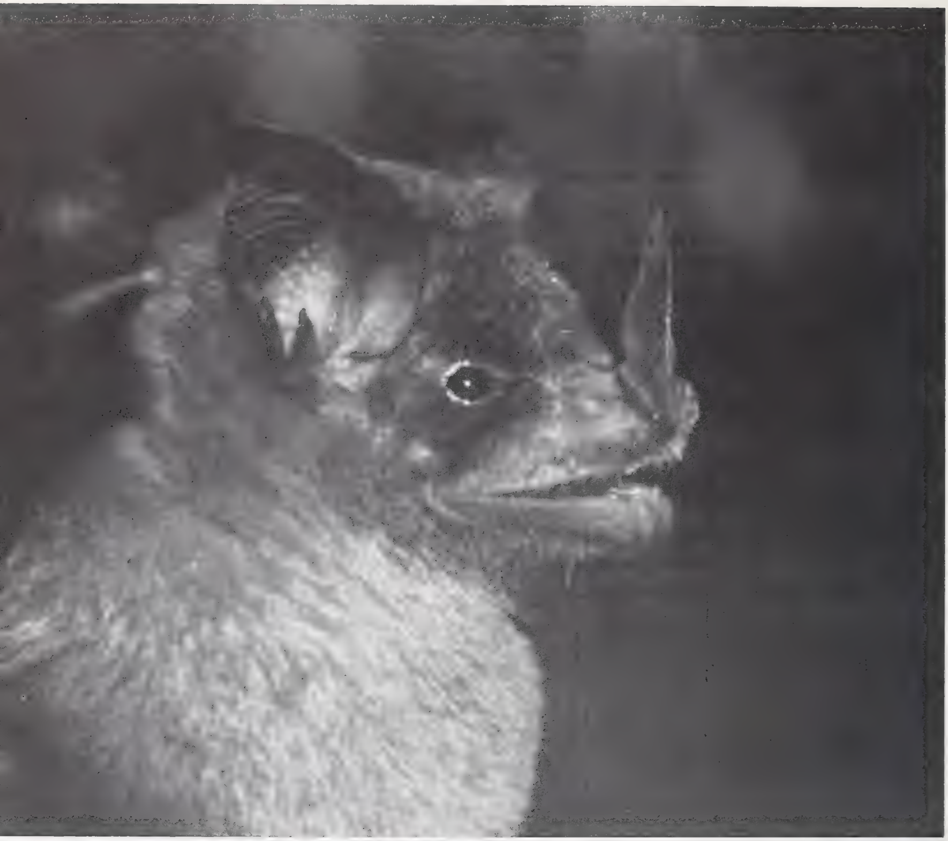


Fig. 27. Nicéforo's large-eared bat, *Micronycteris nicefori. Photo by R. K. LaVal.*

Micronycteris nicefori
Nicéforo's Large-eared Bat

These large-eared bats are found from Belize and southeastern Nicaragua along the Caribbean coast of Central America to Amazonian Brazil in South America (Fig. 27). The species is monotypic.

This species has been collected mainly from forested areas, but is also known from agricultural habitats (Williams and Genoways 1980). Roosting sites include hollow trees, mines, and buildings (Handley 1966). These bats feed on insects and fruit according to Goodwin and Greenhall (1961). The reproductive cycle is unknown.

LaVal (1977) reported capturing six at La Selva in 1973 and 1974; these were the first records from Costa Rica.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU].

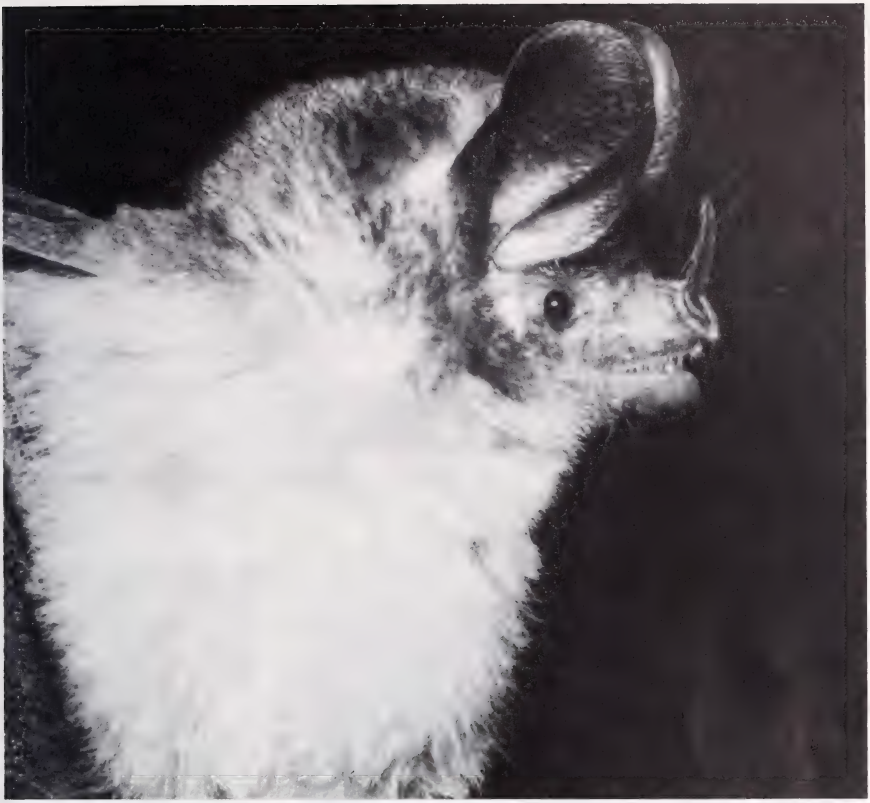


Fig. 28. Schmidt's large-eared bat, *Micronycteris schmidtorum. Photo by B. L. Clauson.*

Micronycteris schmidtorum
Schmidt's Large-eared Bat

Schmidt's large-eared bat, a monotypic species, ranges from Cozumel Island, Mexico, south to Venezuela (Fig. 28). Information on natural history is scanty. Handley's (1976) Venezuelan collection includes specimens from a variety of habitat types. He also reported individuals roosting in tree holes, and they have been taken from hollow trees in Costa Rica (Starrett and Casebeer 1968). This species is insectivorous, but Gardner (1977) also suggested that individuals may take fruit on occasion. Nothing is known about the reproductive cycle.

Starrett and Casebeer (1968) reported the first Costa Rican specimens from Guanacaste Province. Mares and Wilson (1971) reported the first La Selva record. Our single specimen from Braulio Carrillo was netted in primary forest at 300 m.

An adult male bat fly, *Trichobius* sp., was collected from *M. schmidtorum.*

Specimens examined (2)—7.3 mi SE of Puerto Viejo [1 female, TTU]; 11 km S, 4.5 km W of Puerto Viejo, 300 m [1 male, USNM].

Mimon cozumelae
Cozumel Spear-nosed Bat

Cozumel spear-nosed bats are found from Oaxaca and Veracruz, Mexico, to Colombia (Fig. 29). The species is monotypic. *Mimon cozumelae* is sometimes considered a subspecies of *M. bennettii*, a species otherwise confined to South America. A systematic review of this relationship would be in order.

This species normally is found in primary forest. Roosts have been found in caves, mines, culverts (Handley 1966), and hollow logs (LaVal 1977). Gardner (1977) suggested that the diet includes insects and fruit. Wilson (1979) noted that this species produces a single young per year, at the beginning of the rainy season.

The first specimen from La Selva and from Costa Rica was reported by Gardner et al. (1970). We caught another in 1973, and LaVal and Fitch (1977) reported 16 from La Selva. All were taken in primary forest.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 males, MSB].

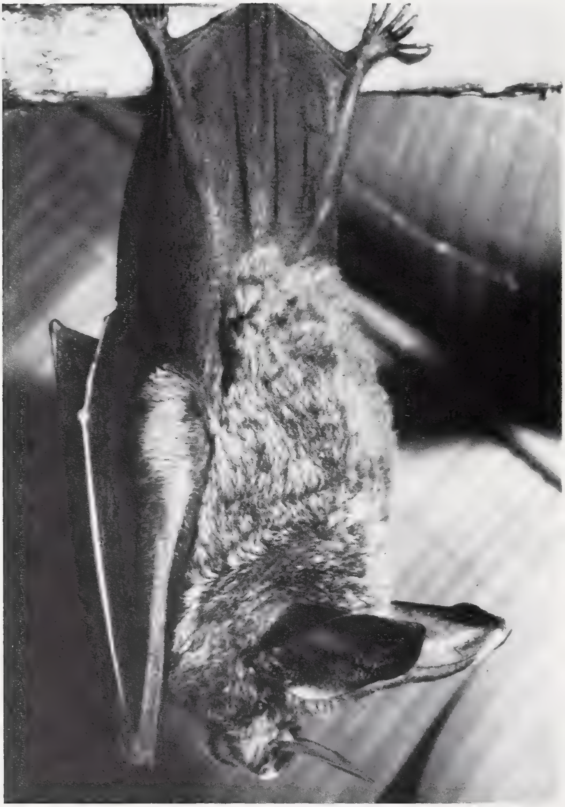


Fig. 29. Cozumel spear-nosed bat, *Mimon cozumelae. Photo by R. K. LaVal.*

Mimon crenulatum
Striped Spear-nosed Bat

Striped spear-nosed bats are found from Chiapas and the Yucatán Peninsula, Mexico, to Brazil (Fig. 30). The subspecies *Mimon crenulatum keenani* is found throughout Central America.

Primarily an inhabitant of forested areas, this species also is known from banana groves (Gardner et al. 1970). Roosts have been found in hollow trees and buildings (Goodwin and Greenhall 1961). Apparently this species is known to eat only insects (Gardner 1977). Reproductive data are too few to speculate on the cycle, but pregnant females are known from Costa Rica at the beginning of the rainy season (Wilson 1979).

Striped spear-nosed bats first were reported from Costa Rica by Gardner et al. (1970) by four specimens from Cariari. LaVal (1977) took 10 individuals in bat traps in primary forest. We obtained one species of bat fly, *Basilia tiptoni* (1 male, 1 female), from *M. crenulatum* at La Selva.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, MSB].

Additional record (1)—2.5 km SE of Puerto Viejo [1 female, TCWC].

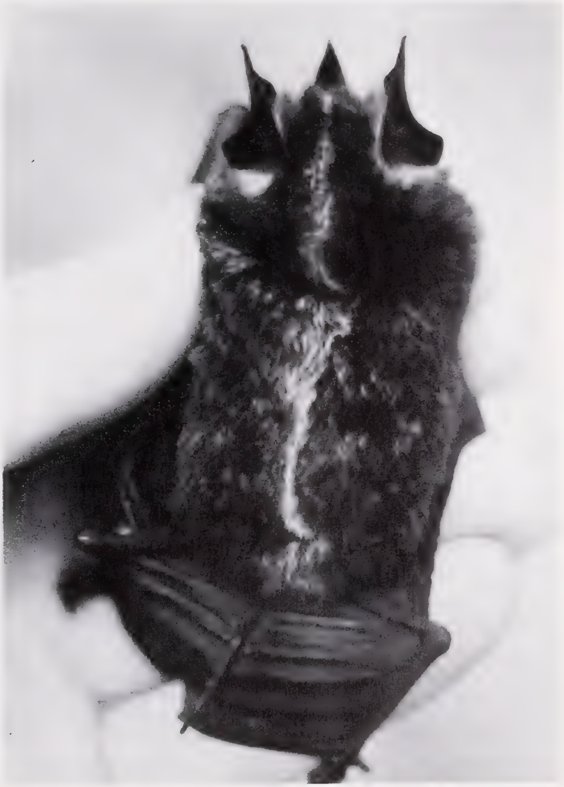


Fig. 30. Striped spear-nosed bat, *Mimon crenulatum*. *Photo by R. K. LaVal.*

Phylloderma stenops
Northern Spear-nosed Bat

Northern spear-nosed bats are found from Chiapas, Mexico, to Brazil (Fig. 31). The Costa Rican subspecies, *Phylloderma stenops septentrionalis*, occurs throughout Central America and was originally described as a distinct species.

This poorly known bat has been recorded from a variety of forested and agricultural habitats, but little information on its biology is available. Roosts are as yet unknown. Food items include insect and plant materials (Jeanne 1970; LaVal 1977). The reproductive cycle is unknown, but LaVal (1977) reported capturing a pregnant female during the dry season (early February) in Costa Rica.

This species first was recorded from Costa Rica by LaVal (1977), who caught an adult female in a bat trap alongside a small stream at La Selva. She was pregnant with a single embryo, 33 mm in crown-rump length, on 9 February 1974. One species of bat fly, *Strebla christinae* (4 males), was collected from this bat.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, KU].

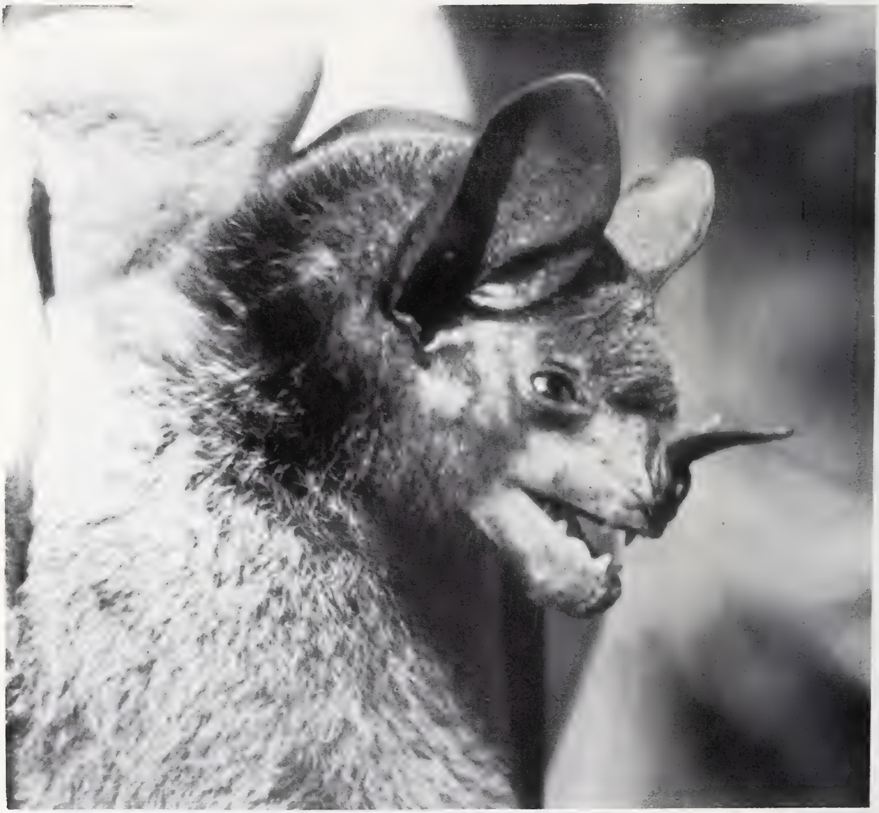


Fig. 31. Northern spear-nosed bat, *Phylloderma stenops. Photo by R. K. LaVal.*

Phyllostomus discolor
Pale Spear-nosed Bat

Pale spear-nosed bats are found from Oaxaca and Veracruz, Mexico, throughout Central America to northern Argentina (Fig. 32). The Costa Rican subspecies, *Phyllostomus discolor verrucosus*, occurs throughout Central America.

This species is associated with a variety of habitats (Williams and Genoways 1980). Roosting sites include hollow trees and caves (Goodwin and Greenhall 1961). Food items include insects, fruit, flowers, pollen, and nectar (Gardner 1977). Despite numerous records of this common species, the reproductive cycle remains enigmatic. Heithaus et al. (1975) suggested that *P. discolor* may be monestrous in Costa Rica.

Davis and Carter (1962) reported a male from Guanacaste Province. LaVal and Fitch (1977) captured one at La Selva, but apparently there are no preserved specimens from the Caribbean lowlands of Costa Rica.

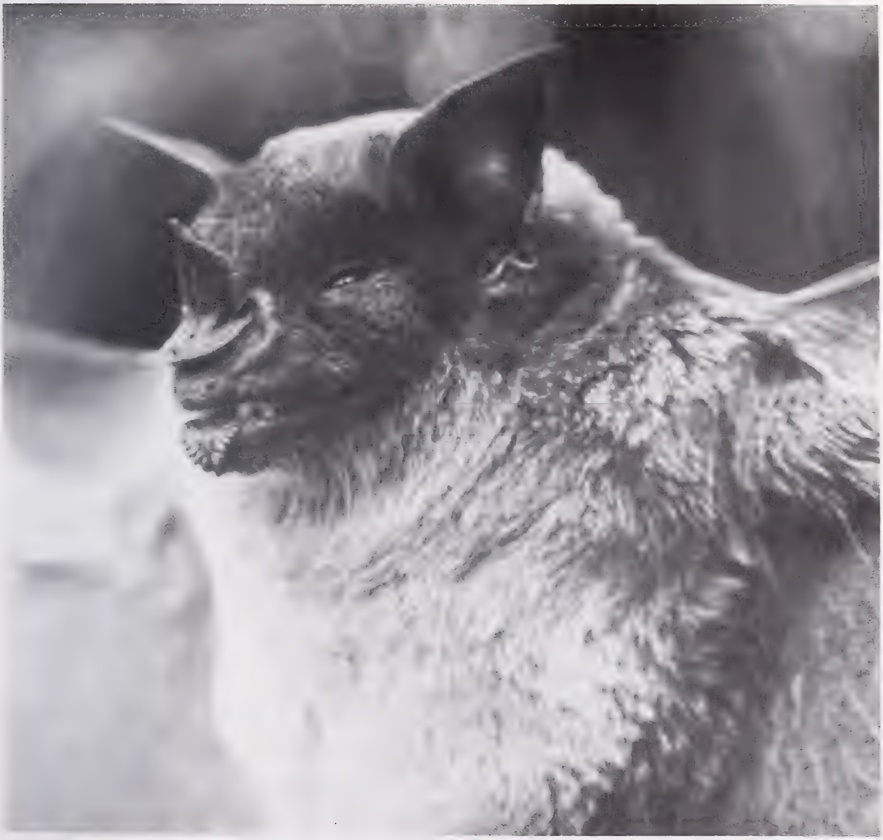


Fig. 32. Pale spear-nosed bat, *Phyllostomus discolor. Photo by R. K. LaVal.*

Phyllostomus hastatus
Big Spear-nosed Bat

Big spear-nosed bats are known from Honduras to Brazil (Fig. 33). The Costa Rican subspecies, *Phyllostomus hastatus panamensis*, is found throughout Central America.

This widespread species has been reported from a number of habitats. Roosting sites include caves, hollow trees, buildings, termite nests, thatched roofs, and foliage (Tuttle 1976). Like other members of the genus, *P. hastatus* feeds on a wide variety of items including insects, small vertebrates, fruit, flowers, nectar, and pollen (Gardner 1977). Wilson (1979) suggested a geographically variable reproductive pattern with some populations monestrous and others bimodally polyestrous.

We captured a single, nonreproductive adult female at La Selva on 1 August 1988 in the clearing around the field station. Although this species is presumed to be widespread in Costa Rica, there are few published records or specimens from the country. Starrett and de la Torre (1964) reported two specimens from Turrialba. LaVal and Fitch (1977) captured one individual at La Selva.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 males, LACM].

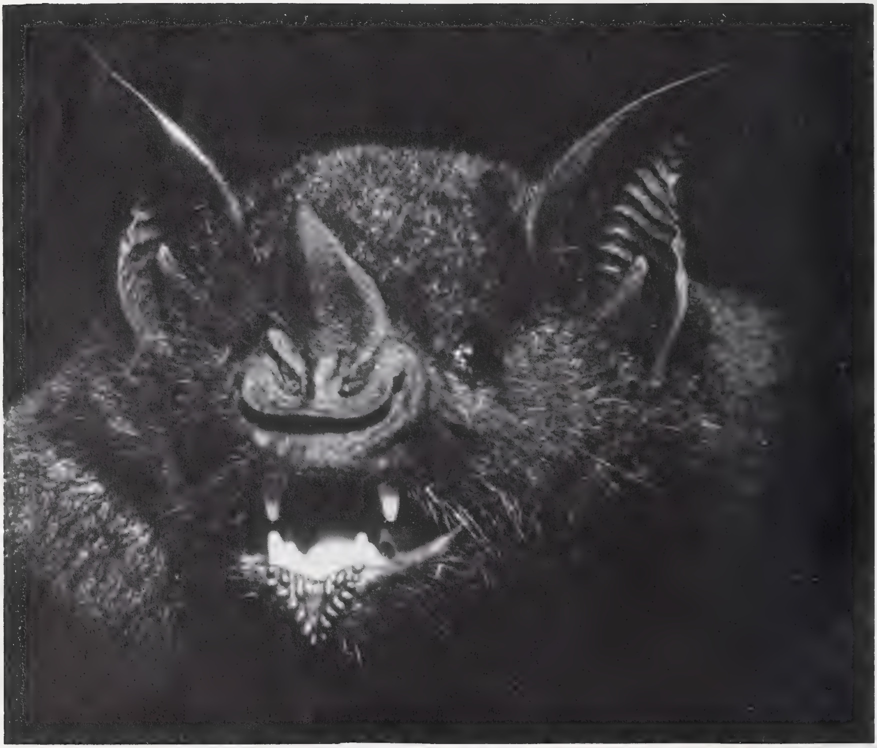


Fig. 33. Big spear-nosed bat, *Phyllostomus hastatus. Photo by B. L. Clauson.*

Tonatia bidens
Spix's Round-eared Bat

Spix's round-eared bats are found from eastern Guatemala to Paraguay (Fig. 34). The recent taxon is monotypic, although there is a fossil subspecies known from Jamaica (Koopman 1976).

This is basically a species of primary forest, but there are records from agricultural areas (Handley 1976). The only known roosts are in hollow trees (Goodwin and Greenhall 1961). Fruit and insects have been reported as food items (Gardner 1977). The reproductive pattern is likely one of bimodal polyestry (Wilson 1979).

Goodwin (1946) reported the species from Palmar, and Gardner et al. (1970) added a specimen from Quepos, both in the Pacific lowlands. LaVal (1977) captured 15 from La Selva. Our specimens from Braulio Carrillo were mist-netted over streams and trails in primary forest.

Bat flies collected from *Tonatia bidens* at La Selva include *Strebla galindoi* (4 males, 2 females) and an undescribed species of *Trichobius* (7 males, 12 females).

Specimens examined (8)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 2 males, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [2 males, 2 females, USNM; 1 female, UNA].

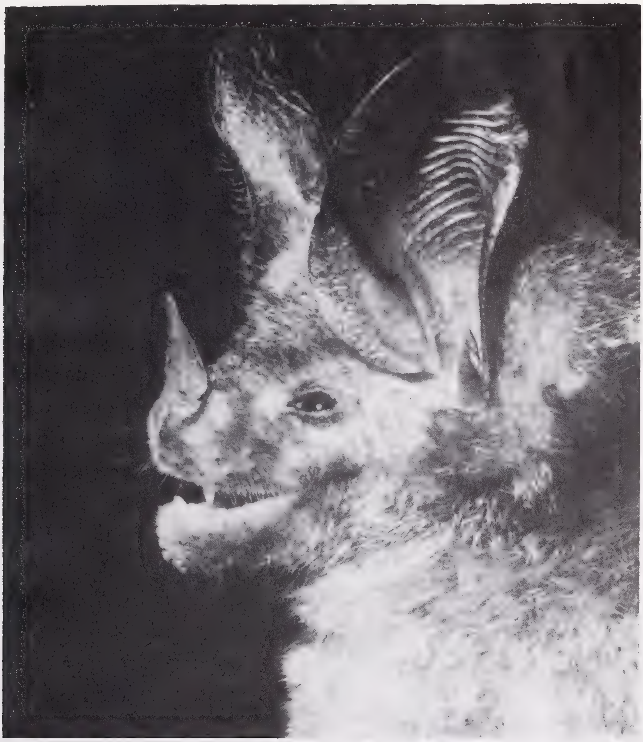


Fig. 34. Spix's round-eared bat, *Tonatia bidens. Photo by B. L. Clauson.*

Tonatia brasiliensis
Pygmy Round-eared Bat

Pygmy round-eared bats are distributed from Veracruz, Mexico, to Brazil (Fig. 35). The species is monotypic although, at one time, four separate species were recognized. Names previously used for this species in Costa Rica include *Tonatia minuta* and *T. nicaraguae*.

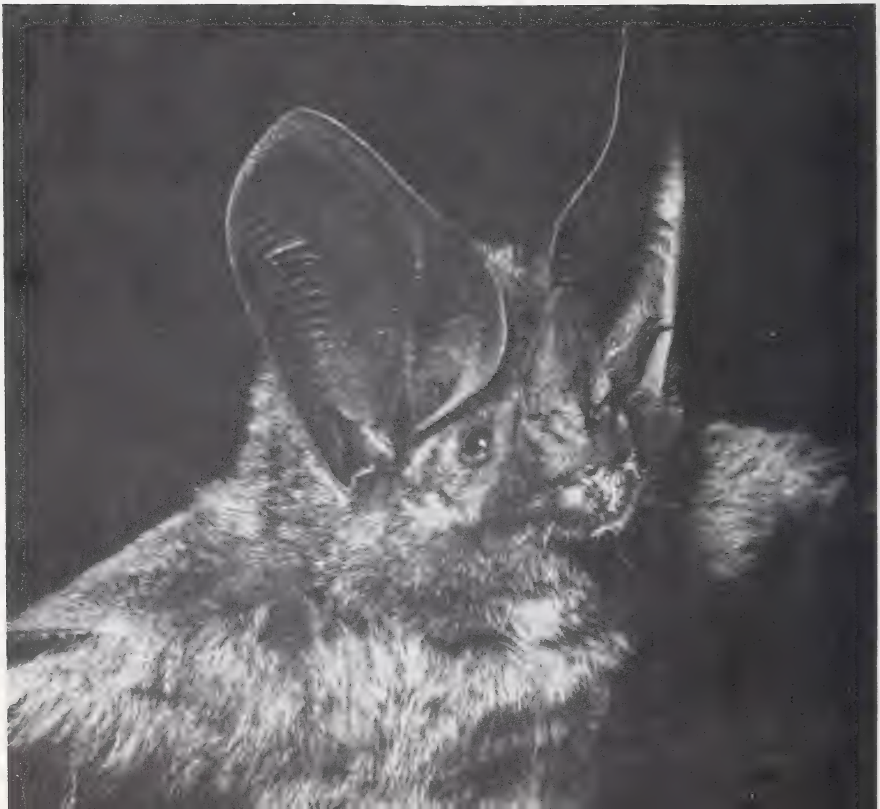
In Costa Rica, this species usually is found in forested habitats, but it is known from agricultural areas as well. The only known roosting sites are termite nests (Goodwin and Greenhall 1961). Gardner (1977) suggested that the species probably feeds on insects and fruit. These bats probably have a bimodally polyestrous reproductive cycle (Wilson 1979).

This species was first recorded from Costa Rica by Gardner et al. (1970), based on specimens from the Osa Peninsula and from Cariari in Limón Province. LaVal (1977) captured eight at La Selva, two of which were pregnant females, one in February and one in April. Our specimen was captured using a mist net set over a small stream in an old clearing at 270 m in Parque Nacional Braulio Carrillo.

Bat flies taken from *T. brasiliensis* were *Mastoptera* sp. (*minuta* complex; 2 males and 2 females).

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM].

Fig. 35. Pygmy round-eared bat, *Tonatia brasiliensis*. *Photo by B. L. Clauson.*



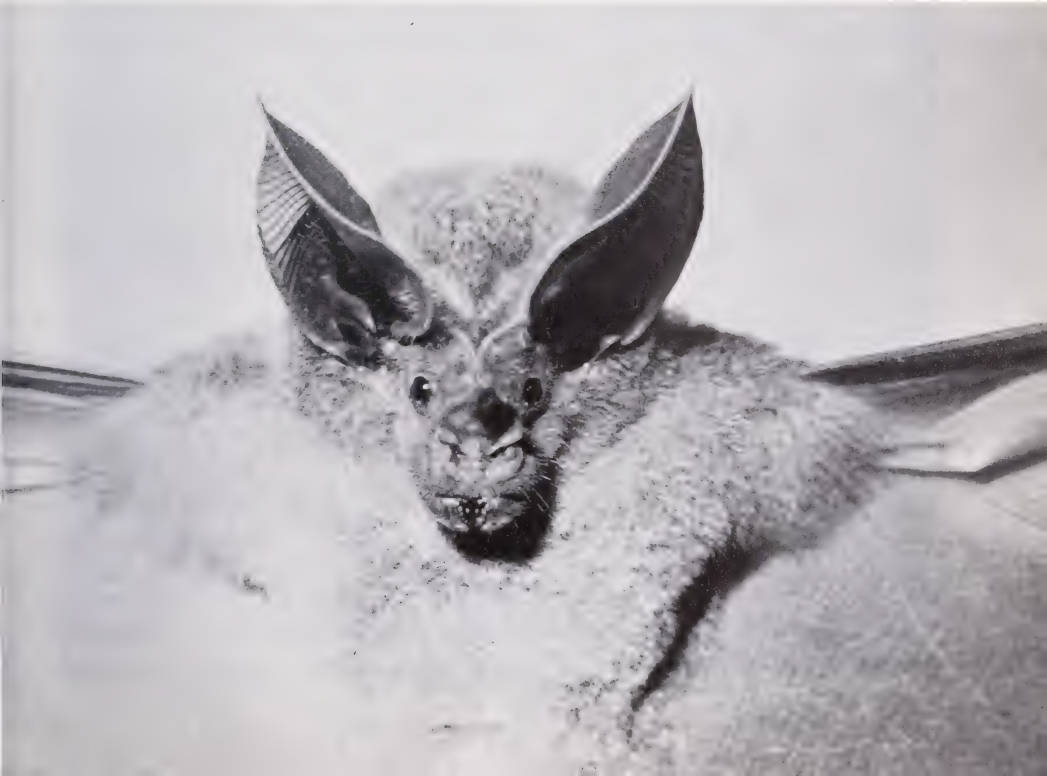
Tonatia silvicola
D'Orbigny's Round-eared Bat

D'Orbigny's round-eared bats are known from Honduras to northern Argentina (Fig. 36). The single subspecies in Costa Rica, *Tonatia silvicola centralis*, also is known from Nicaragua and Honduras (Davis and Carter 1978).

This species has been collected in a variety of habitats ranging from primary forest to agricultural clearings (Hill 1964). Termite nests and tree holes are used as roosting sites (McCarthy et al. 1983; Graham 1988). Insects and fruit are eaten (Fleming et al. 1972). Wilson (1979) reported evidence of only one young per year for this species.

Although several individuals were captured in Guanacaste by various OTS participants in the early 1970's, apparently no specimens were preserved. LaVal (1977) captured one at La Selva, but also did not preserve it. It is possible that there are no preserved specimens of this species available from Costa Rica.

Fig. 36. D'Orbigny's round-eared bat, *Tonatia silvicola. Photo by D. E. Wilson.*



Trachops cirrhosus
Fringe-lipped Bat

Fringe-lipped bats are found from Oaxaca and Veracruz, Mexico, to Brazil (Fig. 37). The nominate subspecies is found throughout Costa Rica, and extends southward into South America.

This is a bat of forested regions, and is known to frequent streams and swampy areas (Tuttle 1970). Caves, houses, culverts, and hollow trees are used as roosting sites (Handley 1966). In addition to feeding on insects and lizards, these bats are specialists on frogs (Tuttle and Ryan 1981). The reproductive cycle is poorly known.

The fringe-lipped bat first was recorded from Costa Rica by Davis and Carter (1962), who captured a single female in Guanacaste. Starrett and Casebeer (1968) added numerous specimens from the Pacific versant. Gardner et al. (1970) reported the first specimen from La Selva. We have netted individuals infrequently at La Selva over the years. The specimen from Parque Nacional Braulio Carrillo was taken in a mist net over a small stream in an old clearing. One species of bat fly, an undescribed *Trichobius* closely related to *T. ethophalalus* (1 male, 1 female), was collected from a single *T. cirrhosus* at La Selva.

Specimens examined (5)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 males, 1 sex ?, MSB]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, USNM]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [1 female, UNA].

Vampyrum spectrum
False Vampire Bat

False vampire bats are found from Veracruz, Mexico, to southwestern Brazil (Fig. 38). The species is monotypic.

Although these predatory bats normally occur in small numbers in primary forest, they have been recorded from a wide variety of habitats (Navarro L. and Wilson 1982). Vehrencamp et al. (1977) studied food habits of a pair of false vampire bats found using a hollow tree roost in Guanacaste Province by studying remains of prey species. They documented predation on a variety of small birds and speculated on foraging behavior. Other prey items include rodents, other bats, and possibly large insects (Bradbury 1983b; McCarthy 1987). Details of the reproductive cycle are unknown.

The first Costa Rican specimen of *Vampyrum spectrum* was taken at Lepanto on the Nicoya Peninsula by a German physician, Dr. Carl Hoffmann, who had moved to Costa Rica in 1858. Casebeer et al. (1963) captured the first specimen from La Selva and the Caribbean lowlands of Costa Rica in 1961. We captured an adult female in primary forest at La Selva in July 1973, and an adult male and lactating female there on 8 July 1974. Additionally, Levey (in litt.) captured one on the path just over the Sura bridge at 2330 h on 5 August 1981, and Reid (in litt.) captured a female near the field station on 7 December 1988. In Parque Nacional Braulio Carrillo, we caught a single adult female in a mist net set on a ridgetop trail in good forest above the Río Cantarrana at 300 m. She made several passing flights near a cloth bag containing other live bats before becoming en-

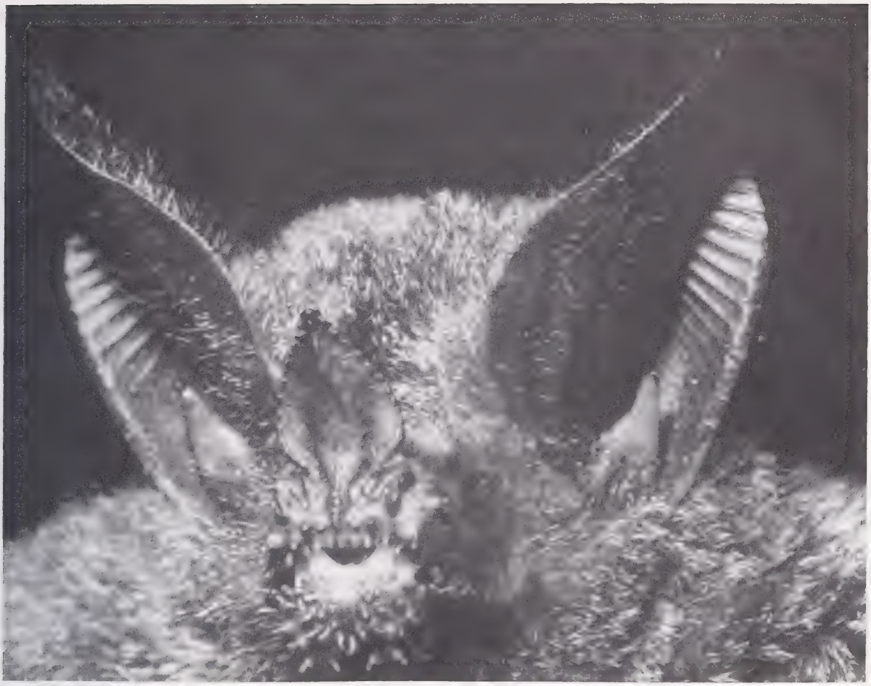


Fig. 37. Fringe-lipped bat, *Trachops cirrhosus. Photo by B. L. Clauson.*

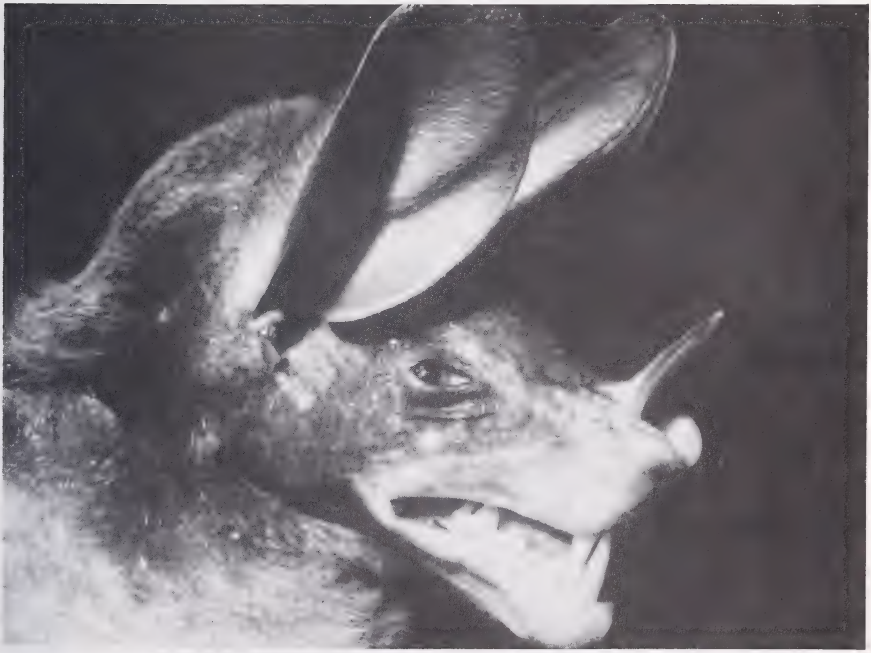


Fig. 38. False vampire bat, *Vampyrum spectrum. Photo by B. L. Clauson.*

tangled in the nearby net. LaVal and Fitch (1977) reported catching four false vampires at La Selva during their study.

Specimens examined (3)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 female, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 300 m [1 female, USNM].

Subfamily Glossophaginae

Anoura cultrata
Handley's Tailless Bat

Handley's tailless bat reaches the northern limit of its known distribution in Costa Rica; it occurs southward in South America along the Andes to Bolivia (Fig. 39). *Anoura cultrata* is monotypic (Nagorsen and Tamsitt 1981), although specimens from the Cordillera de Talamanca originally were named as a separate species, *A. werckleae* (Starrett 1969).

Curiously enough, Handley's tailless bats have a small but obvious tail. This species occupies a variety of habitats, and has been taken at 2,600 m, near the upper elevational limits known for bats in Costa Rica (Gardner et al. 1970). The only reported roosting sites are in caves (Handley 1976). Food items include pollen, nectar, and insects (Gardner 1977). The reproductive cycle is unknown, but available records were summarized by Tamsitt and Nagorsen (1982).

Carter et al. (1966) reported the first Costa Rican specimen, a male from Alajuela Province. Gardner et al. (1970) recorded a female from Vara Blanca, near Braulio Carrillo. Our specimens were taken in mist nets set over small streams in old clearings. Ectoparasites collected from *A. cultrata* include the streblid bat flies *Anastrebla mattadeni* (8 males, 2 females) and *Exastinion oculatum* (11 males, 9 females).

Specimens examined (17)—1 km S, 11.5 km W of San Miguel, 680 m [5 males, 6 females, USNM; 4 males, UNA]; 3.5 km S, 11.5 km W of San Miguel, 1,000 m [1 male, USNM]; Vara Blanca [1 female, LSUMZ].

Anoura geoffroyi
Geoffroy's Tailless Bat

Geoffroy's tailless bats are found from Sinaloa and Tamaulipas, Mexico, to northern Argentina (Fig. 40). The Costa Rican subspecies, *Anoura geoffroyi lasiopyga*, is the race occurring in Mexico and Central America.

A variety of habitats are occupied extending over an elevational range up to at least 2,550 m (Handley 1976). Caves and tunnels are used as roosts (Tuttle 1970). These bats are known to eat pollen, nectar, fruit, and insects (Gardner 1977). This species may be seasonally monestrous, an unusual pattern for phyllostomids (Wilson 1979). *Anoura geoffroyi* is the common species on the Pacific slopes and is mostly replaced by *A. cultrata* on the Caribbean slopes.

Although not uncommon in Costa Rica, specimens of this species rarely have been recorded in the literature. Mares and Wilson (1971) listed 3 from Puntarenas Province, and LaVal (1977) added 13 from Monteverde. Our single specimen came from a mist net set in an old clearing bordered by a small stream.

Specimen examined (1)—5 km E of Vara Blanca, 2,050 m [1 female, USNM].

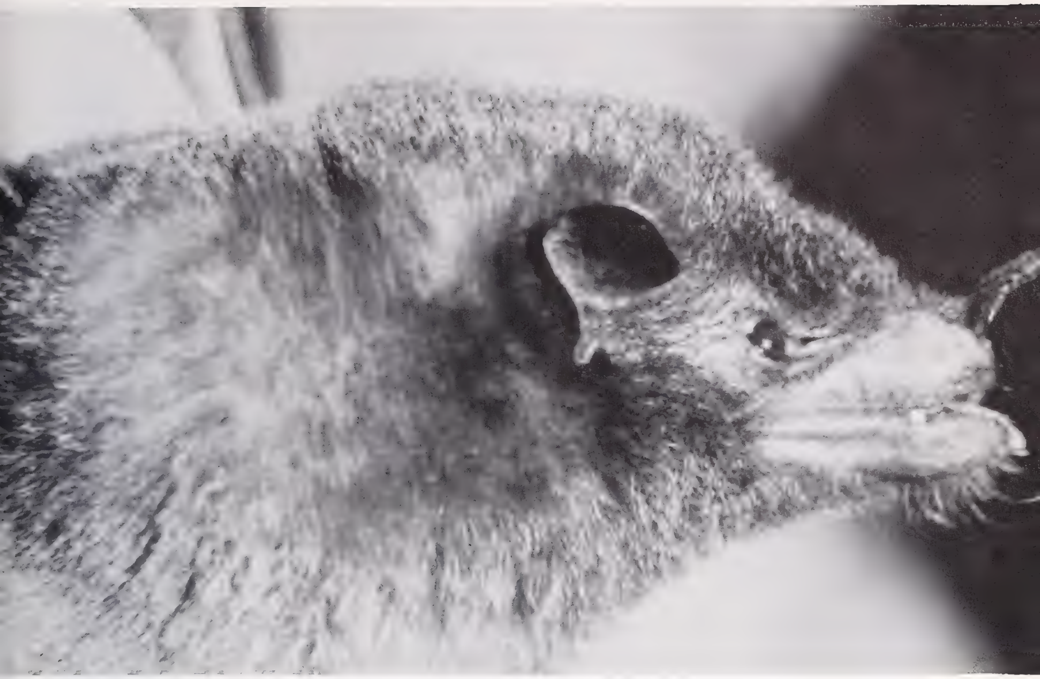


Fig. 39. Handley's tailless bat, *Anoura cultrata. Photo by R. K. LaVal.*

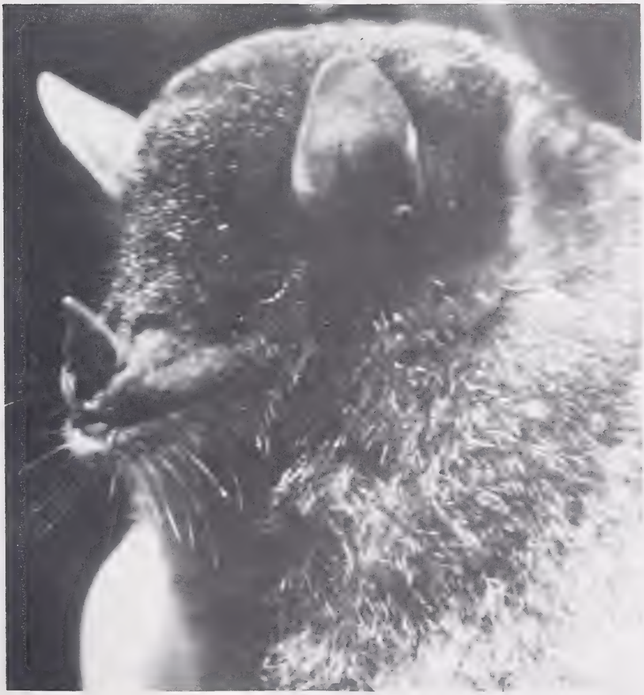


Fig. 40. Geoffroy's tailless bat, *Anoura geoffroyi. Photo by R. K. LaVal.*

Choeroniscus godmani
Godman's Bat

Godman's bats are found from Sinaloa, Mexico, to Suriname (Fig. 41). The species is monotypic.

These bats occupy a variety of habitats ranging from primary forest to agricultural areas; roosting sites have not been recorded. Food probably includes pollen, nectar, and insects (Gardner 1977). Other than the observation that young seem to be weaned at the beginning of the rainy season, little is known of the reproductive cycle (Wilson 1979).

Goodwin (1946) listed four specimens from San José Province and Gardner et al. (1970) added four more from Cartago and Guanacaste Provinces. LaVal and Fitch (1977) captured and released three at La Selva; however, none were preserved.

Glossophaga commissarisi
Commissaris' Long-tongued Bat

Commissaris' long-tongued bats occur from Sinaloa and Veracruz, Mexico, to Brazil and Peru. The nominate subspecies, *Glossophaga commissarisi commissarisi*, is found throughout Central America.

These bats have been collected in a variety of habitats ranging from primary forest to banana groves and clearings. Known roost sites seem to be limited to caves and tunnels (Jones et al. 1972), although we found them to be common where there are no caves or tunnels. Food includes insects, fruit, pollen, and nectar (Gardner 1977). The reproductive cycle is one of bimodal polyestry (Wilson 1979).

This species is quite common at La Selva, where it first was recorded by Mares and Wilson (1971). LaVal and Fitch (1977) captured 81 there. Curiously, we did not encounter *G. commissarisi* in Braulio Carrillo.

Specimens examined (12)—Puerto Viejo, Río Sarapiquí, 300 ft [2 females, UMMZ]; Puerto Viejo, 100 m [1 male, KU]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 5 males, 3 females, MSB].

Additional records (1)—3 mi N of Heredia, 5,600 ft [1 male, TCWC].

Glossophaga soricina
Pallas' Long-tongued Bat

Pallas' long-tongued bats are distributed from Sonora, Mexico, to northern Argentina (Fig. 42). The Costa Rican subspecies, *Glossophaga soricina handleyi*, is found throughout Central America.

This is one of the most widespread and abundant species of bats in the tropical lowlands and occurs in almost every available habitat type. It is known to roost in caves, tunnels, hollow trees, buildings, and culverts (Tuttle 1976). Food items include insects, fruit, pollen, nectar, and flowers (Gardner 1977). The reproductive pattern is one of bimodal polyestry (Wilson 1979). Howell (1983) summarized natural history information.

This species is common at La Selva, but less so than *G. commissarisi*. We captured several there in 1973 and 1974, and LaVal and Fitch (1977) recorded 23. Although we did not encounter them in Braulio Carrillo, a specimen taken at

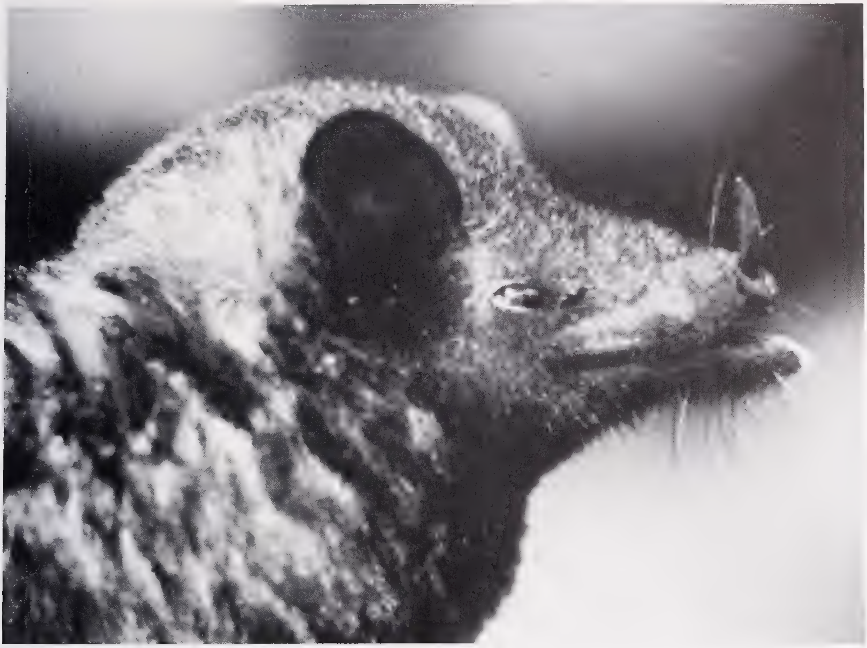


Fig. 41. Godman's bat, *Choeroniscus godmani. Photo by R. K. LaVal.*

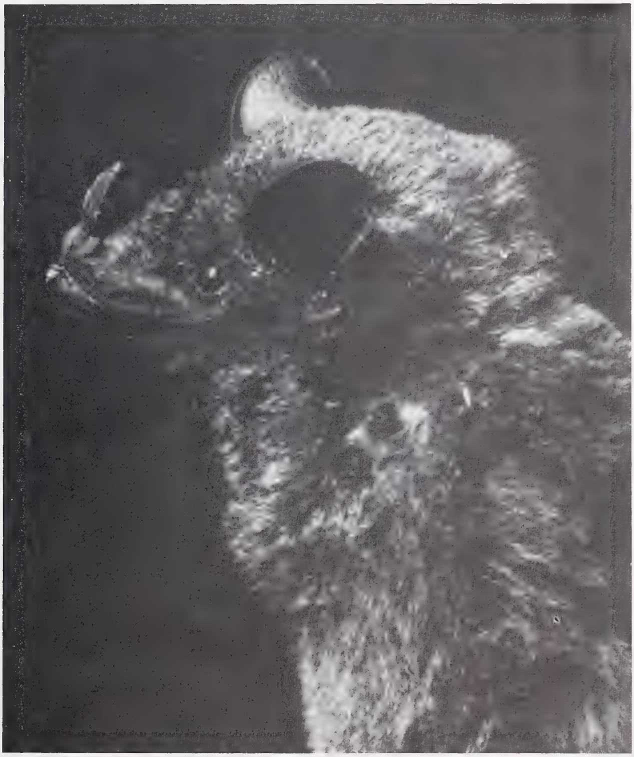


Fig. 42. Pallas' long-tongued bat, *Glossophaga soricina. Photo by B. L. Clauson.*

1,520 m near San José de la Montaña (Starrett and de la Torre 1964) suggests that this species occurs at least seasonally at low and middle elevations there.

Specimen examined (1)—Puerto Viejo, 100 m [1 male, KU].

Additional records (4)—3 mi N of Heredia, 5,600 ft [1 male, 3 females, TCWC]; San José de la Montaña, 1,520 m (Starrett and de la Torre 1964).

Hylonycteris underwoodi
Underwood's Long-tongued Bat

Underwood's long-tongued bats occur from Nayarit and Veracruz, Mexico, to western Panama (Fig. 43). The nominate subspecies, *Hylonycteris underwoodi underwoodi*, is found in Costa Rica and adjacent areas, north to Veracruz.

In general, this species is found in forested habitats, frequently at middle elevations. Roosts have been found in caves, culverts, and hollow logs (Villa-R. 1967). Individuals feed on insects, pollen, and nectar (Gardner 1977). The reproductive cycle is one of bimodal polyestry (Wilson 1979), but pregnant females have been recorded year around (LaVal 1977; LaVal and Fitch 1977). Biology of this species was summarized by Jones and Homan (1974).

The type locality is San José; the first specimens from Vara Blanca, near Parque Nacional Braulio Carrillo, were reported by Gardner et al. (1970). LaVal and Fitch (1977) captured 15 at La Selva. This is the common glossophagine bat in the region, and we netted it in every habitat sampled.

Specimens examined (33)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, LACM; 1 male, 1 female, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [3 males, 2 females, USNM]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, 5 females, USNM; 1 male, UNA]; 3.5 km S, 1.5 km E of San Miguel, 1,000 m [6 females, USNM]; 5 km E of Vara Blanca, 2,050 m [4 males, 1 female, USNM]; Vara Blanca [1 male, 3 females, LSUMZ]; 1 mi W of Vara Blanca [3 females, TTU].

Lichonycteris obscura
Brown Long-nosed Bat

The brown long-nosed bat is a monotypic species found from Belize and Guatemala to Peru and the Guianas.

Little natural history information is available for *Lichonycteris obscura*. Most specimens have been taken in forested habitats. Apparently, roosting sites have not been recorded. The diet includes pollen, nectar, and insects (Gardner 1977). In Costa Rica, pregnant females have been taken in the dry season, but the overall reproductive pattern is unknown.

Goodwin reported two specimens from San José Province. Gardner et al. (1970) recorded the first specimens from the Caribbean lowlands at Cariari, Limón Province. LaVal and Fitch (1977) captured three individuals at La Selva.

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, LACM].

Additional record (1)—2.5 km SE of Puerto Viejo [1 female, TCWC].

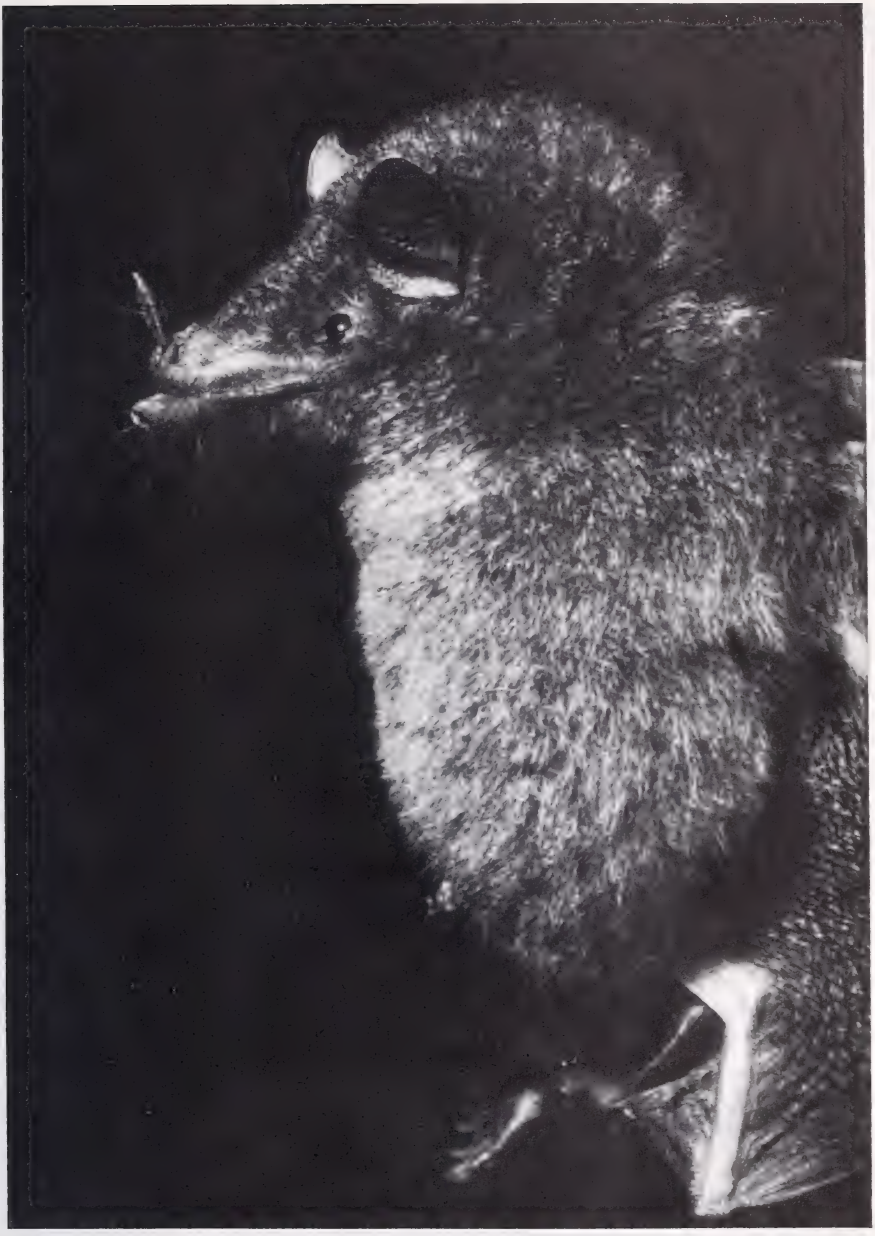


Fig. 43. Underwood's long-tongued bat, *Hylonycteris underwoodi. Photo by B. L. Clauson.*

Lonchophylla robusta
Panama Long-tongued Bat

Panama long-tongued bats occur from Nicaragua to Peru (Fig. 44). This monotypic species normally is found in forested habitats, but it also occurs in agricultural areas. They are known to roost in caves in colonies that can be fairly sizable (Handley 1966). Food items include pollen, nectar, fruit, and insects (Gardner 1977). Nothing is known of the reproductive cycle, although we collected a pregnant female in April in Braulio Carrillo.

The first Costa Rican specimens were collected by J. DeAbate in 1956 (Walton 1963). The first specimens from the Caribbean lowland were reported by Armstrong (1969) from Los Diamantes near Guápiles. LaVal and Fitch (1977) reported 12 from La Selva. We located a roost under a jumble of huge boulders along a stream near the 700-m campsite in Parque Nacional Braulio Carrillo. All our specimens were captured in mist nets set across the stream just above the roost, except for a single individual netted in the forest near 1,000 m.

Bat flies collected from *Lonchophylla robusta* include *Anastrebla nycteridis* (5 males, 4 females), *Eldunnia breviceps* (1 male), and *Trichobius lonchophyllae* (6 males, 4 females).

Specimens examined (16)—7.3 mi SE of Puerto Viejo [2 males, 2 females, TTU]; 1 km S, 11.5 km E of San Miguel, 680 m [3 males, 4 females, USNM; 1 male, 3 females, UNA]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [1 male, USNM].

Additional records—Finca La Selva, 3 km S of Puerto Viejo [MSB].

Subfamily Carollinae

Carollia brevicauda
Silky Short-tailed Bat

Silky short-tailed bats are distributed from San Luis Potosí, Mexico, to southeastern Brazil (Fig. 45). *Carollia brevicauda* is a monotypic species.

This bat is much more common in second growth and disturbed habitats than in primary forest. Roosts are known from caves, tunnels, hollow trees, and culverts (Pine 1972). A variety of fruits and some insects are consumed by these bats (Gardner 1977). They exhibit the bimodal polyestrous reproductive pattern common to many phyllostomids (Wilson 1979).

This species was hidden in the synonymy of *C. perspicillata* until the work of Pine (1972). It frequently has been confused with that species and, in many areas especially at higher elevations, actually may be much more common than *C. perspicillata*. This is the case at La Selva, where LaVal and Fitch (1977) captured 461. In Parque Nacional Braulio Carrillo, it is reasonably common in disturbed habitats up to about 700 m in elevation. Ectoparasites we collected from *C. brevicauda* include two species of streblid bat flies, *Speiseria ambigua* (1 female) and *Trichobius joblingi* (1 female).

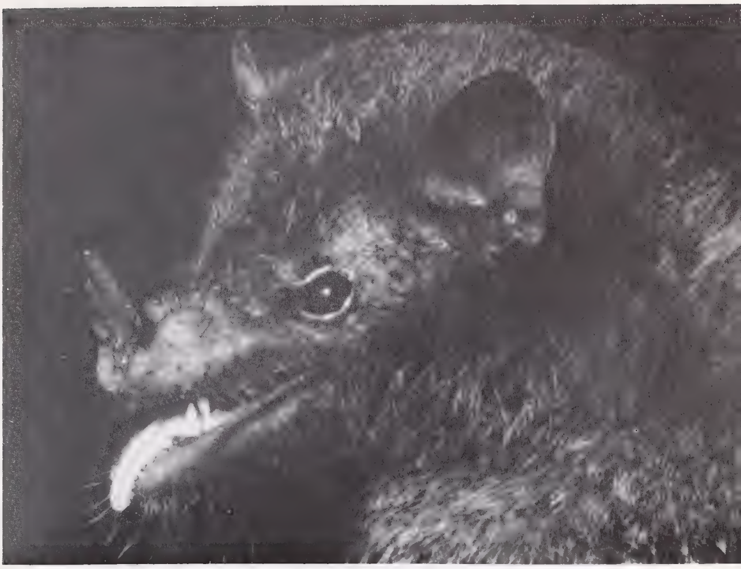


Fig. 44. Panama long-tongued bat, *Lonchophylla robusta. Photo by B. L. Clauson.*

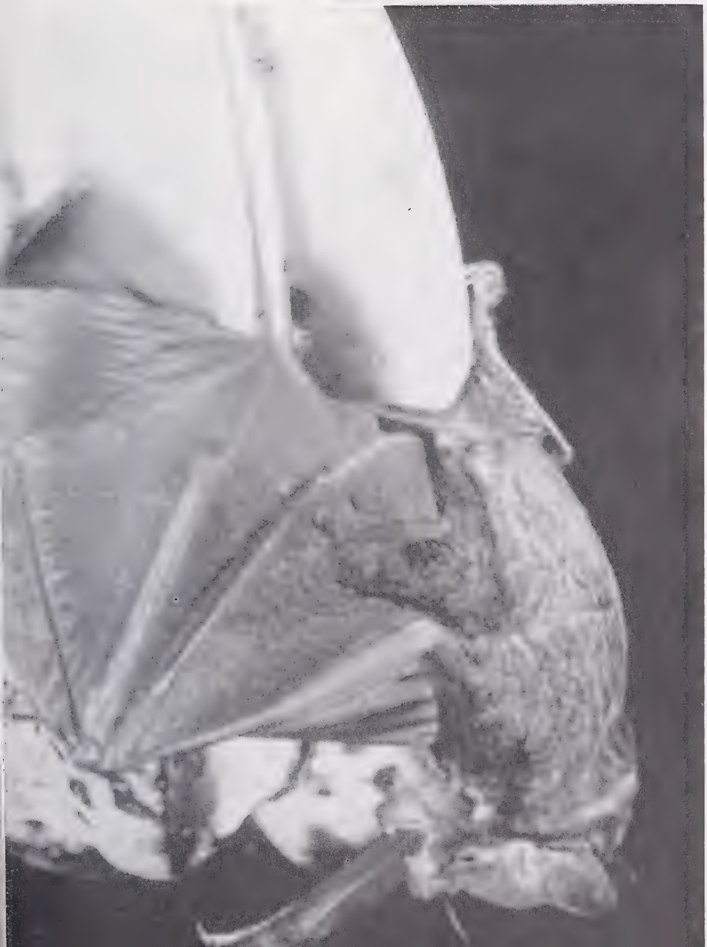


Fig. 45. Silky short-tailed bat, *Carollia brevicauda. Photo by R. K. LaVal.*

Specimens examined (31)—2.5 km SE of Puerto Viejo [2 males, CM; 1 male, TCWC]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [10 males, 8 females, KU; 1 male, MSB]; 7.3 mi SE of Puerto Viejo [1 male, TTU]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM]; 1 km S, 11.5 km E of San Miguel, 680 m [4 males, 2 females, USNM; 1 female, UNA].

Additional records (3)—4 mi W of Puerto Viejo, 300 ft [2 females, TCWC]; 5.5 mi S, 1 mi E of Puerto Viejo, 400 ft [1 female, TCWC].

Carollia castanea
Allen's Short-tailed Bat

Allen's short-tailed bats are found from Honduras to Bolivia (Fig. 46). *Carollia castanea* is a monotypic species.

These bats are more likely to be taken in primary forest than their congeners, but also are common in second growth habitats. Roosting sites include caves, tunnels, hollow trees, and under overhanging roots along stream banks (Pine 1972). They feed on a variety of fruits, and perhaps occasional insects (Gardner 1977). The reproductive cycle is bimodally polyestrous (Wilson 1979).

This species is common throughout lowland Costa Rica. LaVal and Fitch (1977) captured 302 at La Selva. We found it only at the 300-m site in Braulio Carrillo, where we captured specimens in nets set over a stream, and along a trail in hillside primary forest.

Specimens examined (41)—Puerto Viejo, Río Sarapiquí, 300 ft [1 female, FMNH; 3 males, 5 females, KU; 3 males, 2 females, UMMZ]; 2.5 km SE of Puerto Viejo [2 males, 1 female, CM; 2 males, TCWC]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, 4 females, KU; 1 male, 5 females, LACM; 2 females, 1 sex ?, MSB]; 7.3 mi SE of Puerto Viejo [2 females, TTU]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [4 males, 1 female, USNM; 1 male, UNA].

Additional records (3)—5.5 mi S, 1 mi E of Puerto Viejo, ca. 400 ft [3 males, TCWC].

Carollia perspicillata
Seba's Short-tailed Bat

Seba's short-tailed bats are distributed from Puebla, Mexico, to Argentina (Fig. 47). The Costa Rican subspecies, *Carollia perspicillata azteca*, is found throughout Central America.

This is one of the most widespread and abundant species of Neotropical bats. It is particularly common in second growth and disturbed habitats. Roosts are known from caves, tunnels, hollow trees, buildings, culverts, and under large leaves (Pine 1972). These bats specialize on fruits of the genus *Piper*, but take a wide variety of other fruits, and also insects during some seasons (Gardner 1977). The reproductive pattern is the familiar one of bimodal polyestry (Wilson 1979). Fleming (1983a, 1988) summarized the results of more than 10 years of detailed studies of the life history of this species in Costa Rica.

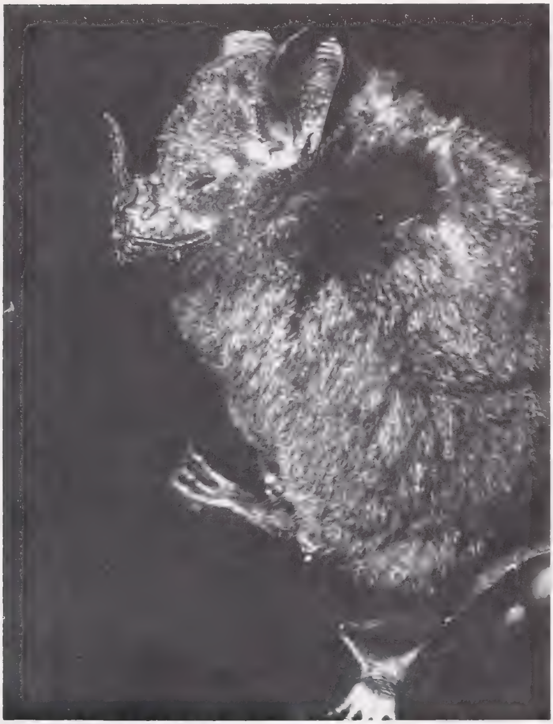


Fig. 46. Allen's short-tailed bat, *Carollia castanea. Photo by B. L. Clauson.*

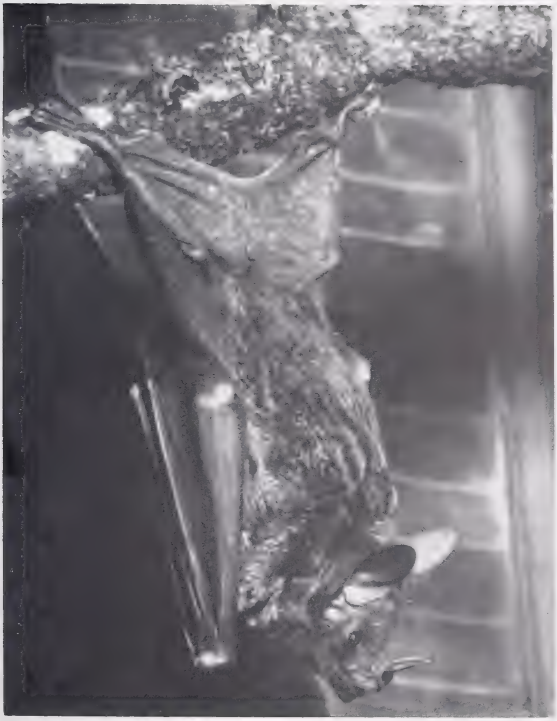


Fig. 47. Seba's short-tailed bat, *Carollia perspicillata. Photo by R. K. LaVal.*

This species is common in the lowlands throughout Costa Rica. LaVal and Fitch (1977) captured 101 at La Selva, and we have found them to be abundant there on many occasions since 1968. We found them to be common in second growth habitats up to 700 m in Parque Nacional Braulio Carrillo. An adult female collected at Puerto Viejo on 14 July 1961 carried a single embryo, 18 mm crown-rump length.

We collected two species of streblid bat flies, *Speiseria ambigua* (1 female) and *Trichobius joblingi* (1 female), from *C. perspicillata*. The biology of three species of bat flies of the family Streblidae, which are host-specific, blood-feeding ectoparasites on *C. perspicillata*, was investigated at La Selva by Fritz (1983). He found that the life cycles of the bat flies are tightly synchronized with the life cycles of their hosts.

Specimens examined (43)—Puerto Viejo, Río Sarapiquí, 100 m [10 males, 3 females, KU; 5 males, 4 females, UMMZ]; 2.5 km SE of Puerto Viejo [2 males, 1 female, CM]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 female, LACM; 2 males, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [6 males, 2 females, USNM]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, 1 female, USNM; 2 males, 2 females, UNA].

Additional records (10)—1.5 mi S of Cariblanco [2 males, 1 sex ?, MVZ]; 4 mi W of Puerto Viejo, 300 ft [3 females, TCWC]; 5.5 mi S, 1 mi E of Puerto Viejo, 400 ft [4 males, TCWC].

Subfamily Stenoderminae

Artibeus jamaicensis
Jamaican Fruit-eating Bat

Jamaican fruit-eating bats are found from Sinaloa and Tamaulipas, Mexico, south through northern South America to Brazil and Paraguay (Fig. 48). Two subspecies are known from Costa Rica, *Artibeus jamaicensis paulus* from Guanacaste Province, and *A. j. richardsoni* from the rest of the country. Although widespread and abundant, species limits and infraspecific variation within this complex of bats are not well understood.

This is one of the most common species of bats throughout tropical America. It is found in most habitat types except perhaps the highest and driest. The known roosting habits are also catholic: caves, tunnels, hollow trees, logs, culverts, bridges, foliage, leaf-tents, and under tree roots (Foster and Timm 1976; Tuttle 1976). Gardner (1977) reported fruits as the primary food source, but flowers, leaves, and occasional insects also are taken. The reproductive cycle is one of bimodal polyestry (Wilson 1979). Morrison (1983) summarized natural history information.

The distribution in Costa Rica is widespread and well documented. This is one of the most common species of bat at La Selva. LaVal and Fitch (1977) captured 111 during their study, and we have captured numerous individuals during OTS field courses. They are found routinely in all habitats at La Selva. In Parque Nacional Braulio Carrillo, we found them to be common up to 700 m.

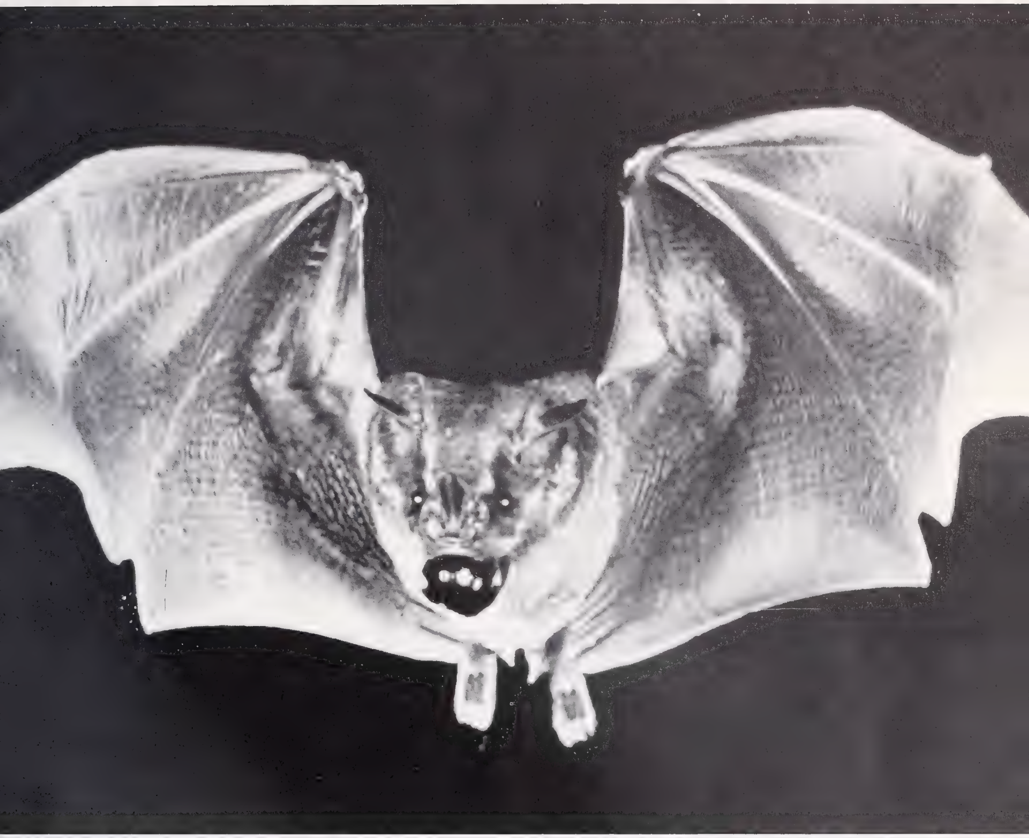


Fig. 48. Jamaican fruit-eating bat, *Artibeus jamaicensis. Photo by M. D. Tuttle.*

Specimens examined (22)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 female, LACM]; Puerto Viejo, Río Sarapiquí, 300 ft [2 females, KU; 7 males, 3 females, UMMZ]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [3 males, 2 females, USNM; 1 female, UNA]; 1 km S, 11.5 km E of San Miguel, 680 m [2 females, USNM].

Additional records (6)—6 mi SSE of Puerto Viejo [3 males, 1 female, TCWC]; 3 mi N of Heredia, 5,600 ft [2 males, TCWC].

Artibeus lituratus
Big Fruit-eating Bat

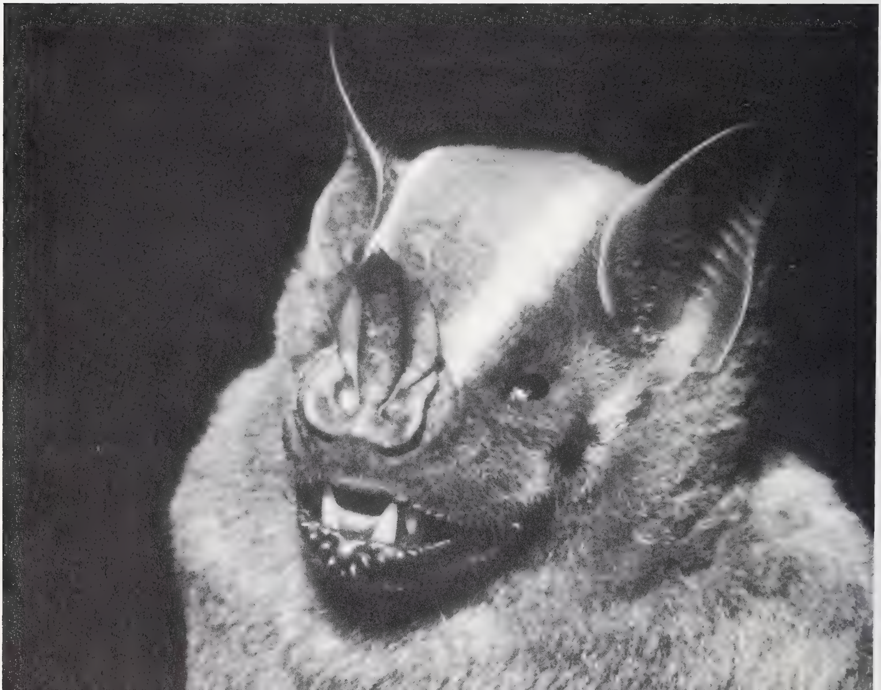
Big fruit-eating bats are found from Sinaloa, Mexico, south through Central America to Argentina in South America (Fig. 49). According to Davis (1984), the single subspecies occurring in Costa Rica is *Artibeus lituratus palmarum*. He recognized *A. intermedius*, formerly considered a subspecies of *A. lituratus*, as a distinct species. *Artibeus intermedius* is more common on the Pacific side of the country.

This species is widespread and locally abundant. The variety of habitats used ranges from dry forest to wet tropical forest. Roosting sites include caves, tunnels, hollow trees, buildings, culverts, foliage, and rock crevices (Goodwin and Greenhall 1961). Although primarily frugivorous, flowers, leaves, and insects also are taken (Gardner 1977). The reproductive cycle is one of bimodal polyestry (Wilson 1979; Willig 1985).

Although found throughout the country, this larger species is less abundant at most sites than *A. jamaicensis*. LaVal and Fitch (1977) took 16 at La Selva. We collected only one from Braulio Carrillo. Frequently, these bats forage higher in the canopy than do *A. jamaicensis*, and are more difficult to capture in ground-level mist nets.

Specimens examined (7)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, 2 females, LACM; 1 male, 1 sex ?, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, UNA]; Puerto Viejo, Río Sarapiquí, 300 ft [1 female, KU].

Fig. 49. Big fruit-eating bat, *Artibeus lituratus. Photo by B. L. Clauson.*



Chiroderma salvini
Salvin's White-lined Bat

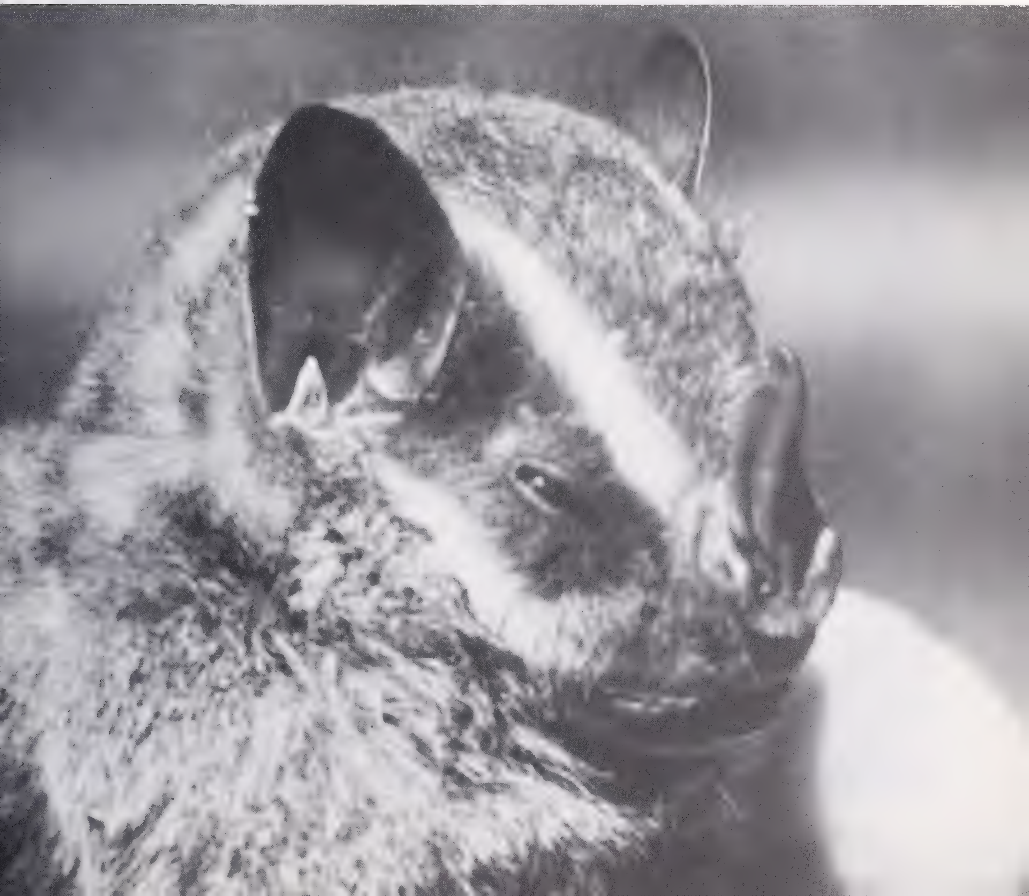
Salvin's white-lined bats are found from Chihuahua, Mexico, south through Central America to Peru and Bolivia (Fig. 50). Only the nominate subspecies, *Chiroderma salvini salvini*, is known to occur in Costa Rica, although Hall's (1981) distribution map suggests that *C. s. scopaeum* may be found in Guanacaste.

This species is found in forested regions, usually at middle or high elevations. They are frugivorous, but details of the food habits are lacking. The reproductive pattern is likely bimodal polyestry (Wilson 1979). Roosting sites are unknown.

Dobson (1878) described *C. salvini* from a specimen collected in Costa Rica by O. Salvin. White-lined bats are also known from near San Vito de Java (Wilson 1983a). Our specimen from 680 m in Parque Nacional Braulio Carrillo is the first record for the northeastern Caribbean slopes. It was a pregnant female, netted over a small stream crossing a pasture area.

Specimen examined (1)—1 km S, 11.5 km E of San Miguel, 680 m [1 female, USNM].

Fig. 50. Salvin's white-lined bat, *Chiroderma salvini. Photo by R. K. LaVal.*



Chiroderma villosum
Shaggy-haired Bat

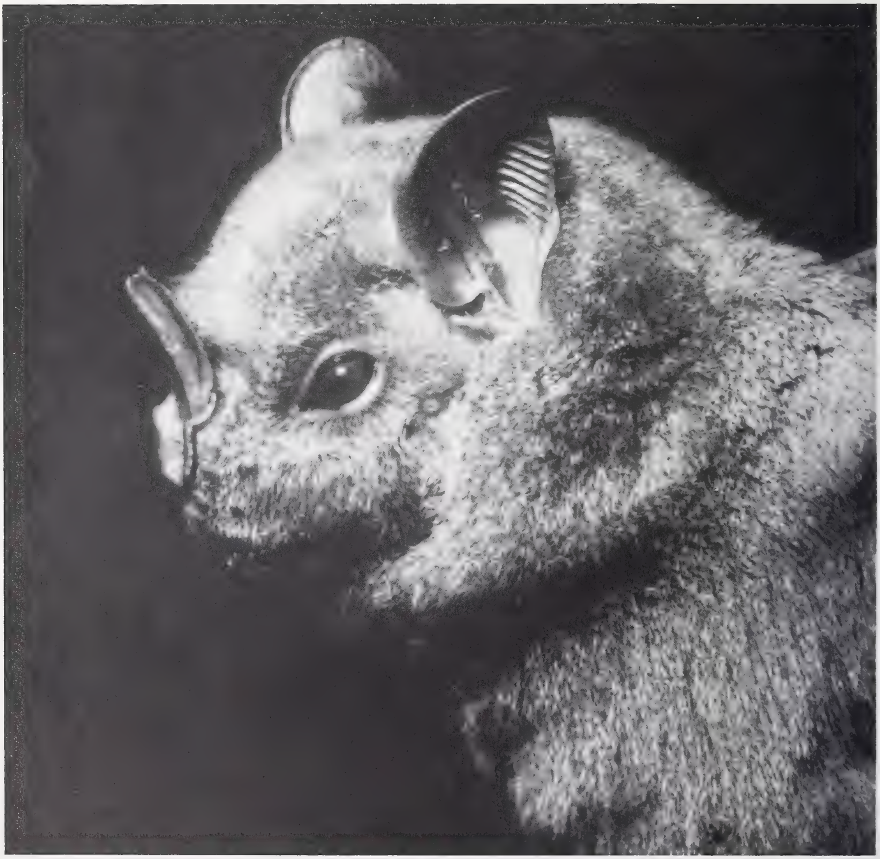
Shaggy-haired bats are found from Veracruz, Mexico, to Brazil (Fig. 51). The Central American subspecies is *Chiroderma villosum jesupi*, the nominate race being restricted to South America and Trinidad.

This species is normally found in primary tropical forests at lower elevations. Roosting sites are unknown. Although presumed to be frugivorous, nothing is known of this bat's food habits. The species is polyestrous, but details of the cycle are unknown.

Goodwin (1946) first reported this species from Costa Rica based on a specimen from Guanacaste. Armstrong (1969) took the first specimen from La Selva, and LaVal and Fitch (1977) added a second.

Specimens examined (6)—Puerto Viejo, Río Sarapiquí, 100 m [1 male, KU; 1 male, 1 female, UMMZ]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, 2 females, LACM].

Fig. 51. Shaggy-haired bat, *Chiroderma villosum. Photo by B. L. Clauson.*



Dermanura azteca
Highland Fruit-eating Bat

Highland fruit-eating bats are known from Sinaloa, Mexico, to western Panama (Fig. 52). The Costa Rican subspecies is *Dermanura azteca major*, which is essentially restricted to Costa Rica and northern Panama. We follow Owen (1987) in recognizing *Dermanura* as a genus distinct from *Artibeus*.

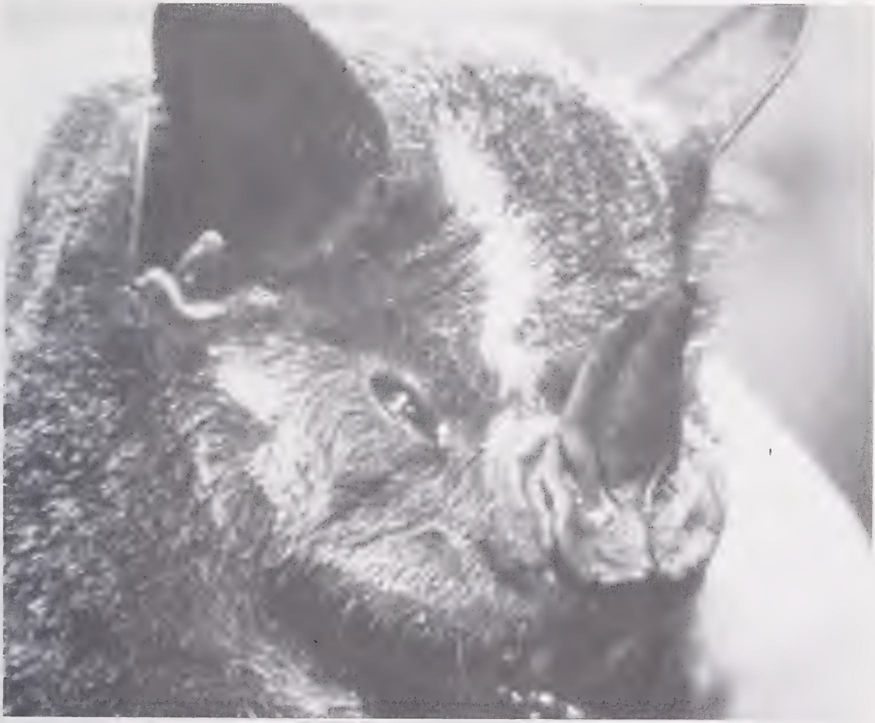
This species is limited to habitats above 1,000 m. Known roosting sites are caves and tunnels (Davis et al. 1964), although it seems likely that this bat also will prove to be a tent-constructor as have all the other previously studied small *Dermanura* (Timm 1987). Food habits are unknown, but the bat is presumed to be frugivorous. Reproductive data are too few to allow speculation on the annual pattern (Wilson 1979). Biology of this species was summarized by Webster and Jones (1982a).

This species had not been recorded previously from the northeastern Caribbean slope of Costa Rica, although it is known from the Talamancas and the Monteverde area (Wilson 1983a). Our specimen from near Vara Blanca was taken from a pasture near a small stream.

Specimens examined (9)—5 km E of Vara Blanca, 2,050 m [1 male, USNM]; 1 mi W of Vara Blanca [2 males, 6 females, TTU].

Additional records (4)—Vara Blanca [2 females, TCWC; 2, LSUMZ].

Fig. 52. Highland fruit-eating bat, *Dermanura azteca. Photo by R. K. LaVal.*



Dermanura hartii
Little Fruit-eating Bat

Little fruit-eating bats are known from Jalisco and Tamaulipas, Mexico, to Bolivia (Fig. 53). *Dermanura hartii* is a monotypic species exhibiting little geographic variation throughout its extensive range. The generic placement, however, has been the subject of much debate. This species has been considered to be the sole member of the genus *Enchisthenes*, a member of the overly inclusive genus *Artibeus*, and most recently a member of the genus *Dermanura* (Owen 1987).

This species occurs primarily in highlands, although there are scattered records from the lowlands. It occurs in a variety of types of forests ranging from dry to quite humid (Handley 1976). Roosting sites have not been reported. Gardner (1977) summarized the feeding habits and suggested figs were an important component of the diet. The few data available on reproduction suggest a bimodal pattern (Wilson 1979).

Armstrong (1969) reported the first record for Costa Rica from Finca Las Cruces in Puntarenas Province. Gardner et al. (1970) listed 19 additional specimens from the country, including the first from Heredia Province.

Specimens examined (5)—Vara Blanca, 1,900 m [1 male, 4 females, LSUMZ].

Dermanura phaeotis
Pygmy Fruit-eating Bat

Pygmy fruit-eating bats are found from Sinaloa and Veracruz, Mexico, south throughout Central America and much of northern South America to Peru (Fig. 54). Two subspecies are known from Costa Rica, the nominate form from the Caribbean versant, and *Dermanura phaeotis palatina* from northwestern Costa Rica. This is an abundant species in Costa Rica and at La Selva, although probably not as abundant there and in many other areas as is *D. watsoni*. These two species are similar in appearance and are often misidentified, both in the field and in museum collections.

Pygmy fruit-eating bats are found in lowland forested areas, both wet and dry (Timm 1985). They modify both banana and *Heliconia* leaves to form tents for roosting sites (Timm 1987). Primarily frugivorous, they occasionally take pollen as well, and have been reported to feed on 11 different species of plants in Costa Rica (Heithaus et al. 1975). The reproductive pattern is one of bimodal polyestry (Timm 1985).

Although *Dermanura phaeotis* are common in Costa Rica, specimens have been confused under a variety of names in the past. LaVal and Fitch (1977) reported that this was one of the most common species of bats they captured at La Selva. We caught only two individuals in Parque Nacional Braulio Carrillo.

Specimens examined (9)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 males, 2 females, KU; 2 males, 1 female, MSB]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, UNA]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, USNM].

Fig. 53. Little fruit-eating bat, *Dermanura hartii.* *Photo by R. K. LaVal.*

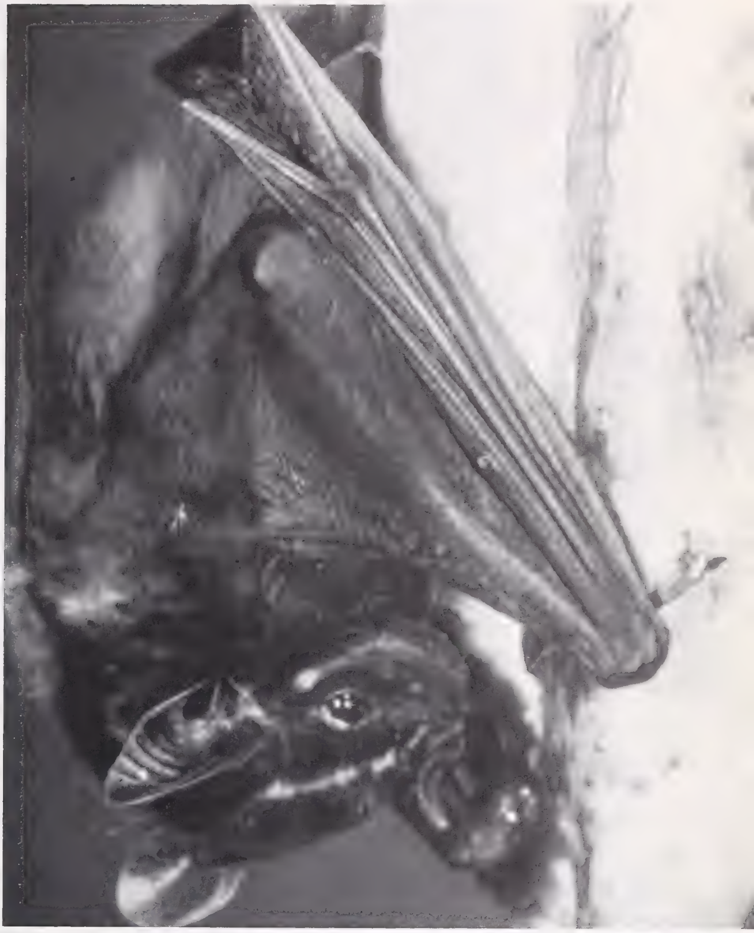
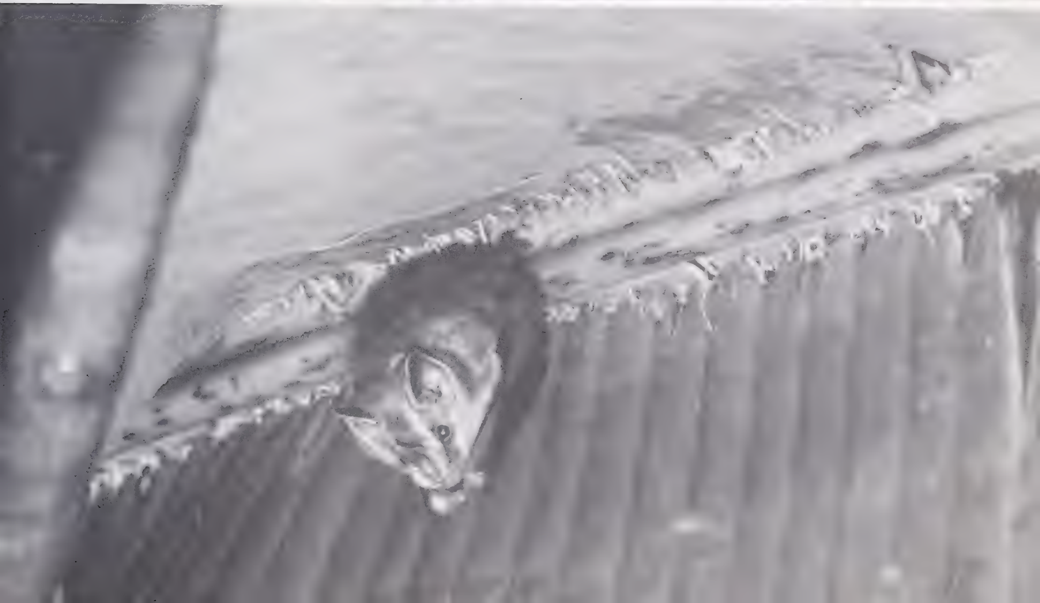


Fig. 54. Pygmy fruit-eating bat, *Dermanura phaeotis.* *Photo by R. M. Timm.*



Dermanura tolteca
Lowland Fruit-eating Bat

Lowland fruit-eating bats are found from Sinaloa, Mexico, to Panama (Fig. 55). Only the nominate subspecies, *Dermanura tolteca tolteca*, occurs in Costa Rica.

The common name is something of a misnomer, as these bats are more frequently caught at middle elevations than in the lowlands. A variety of forested habitats are inhabited, including dry forest. Known roosts include caves, tunnels, buildings, and foliage (Tuttle 1976). Dinerstein (1986) listed the fruit of 17 species of plants in the diet of this species at Monteverde, Costa Rica. Births are spread through much of the year in Mexico, and the usual bimodal polyestrous pattern was confirmed by Dinerstein (1986). Biology of this bat was summarized by Webster and Jones (1982b).

This species is abundant at Monteverde (LaVal and Fitch 1977), and is known from several other localities in Costa Rica (Wilson 1983a). Our specimens from Braulio Carrillo, taken in primary forest, represent the first records for the northeastern Caribbean slope. Two of the three females were pregnant.

Specimens examined (3)—1 km S, 11.5 km E of San Miguel, 680 m [2 females, USNM; 1 female, UNA].

Additional records—Vara Blanca [LSUMZ; Gardner et al. 1970].

Dermanura watsoni
Thomas' Fruit-eating Bat

Thomas' fruit-eating bats are found from Oaxaca and Veracruz, Mexico, through Central America to Colombia (Fig. 56). The species is monotypic. *Dermanura watsoni* has been considered at times to be a subspecies of *D. cinerea*.

Although common in a variety of habitats, this species normally is restricted to forested areas. It seems to be absent from the drier parts of Costa Rica and of Central America in general. This is another species of tent-making bat, modifying large leaves to provide roosting sites (Timm 1987). They are primarily frugivorous (Gardner 1977). The reproductive pattern is bimodal polyestry (Fleming et al. 1972).

These bats are found throughout most of Costa Rica, but apparently do not occur in the Guanacaste lowlands. We collected two from Parque Nacional Braulio Carrillo, both from riparian situations near undisturbed forest.

One species of spinturnicid bat mite, *Periglischrus iheringi*, was collected on *D. watsoni*.

Specimens examined (47)—2.5 km SE of Puerto Viejo [3 males, CM; 1 male, TCWC]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, FMNH; 5 males, 2 females, LACM; 8 males, 4 females, MSB]; Puerto Viejo, Río Sarapiquí, 300 ft [2 males, 4 females, KU; 1 male, 4 females, UMMZ]; 7.3 mi SE of Puerto Viejo [7 males, TTU]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM]; Río Puerto Viejo [1 male, 1 female, KU]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, USNM; 1 male, UNA].

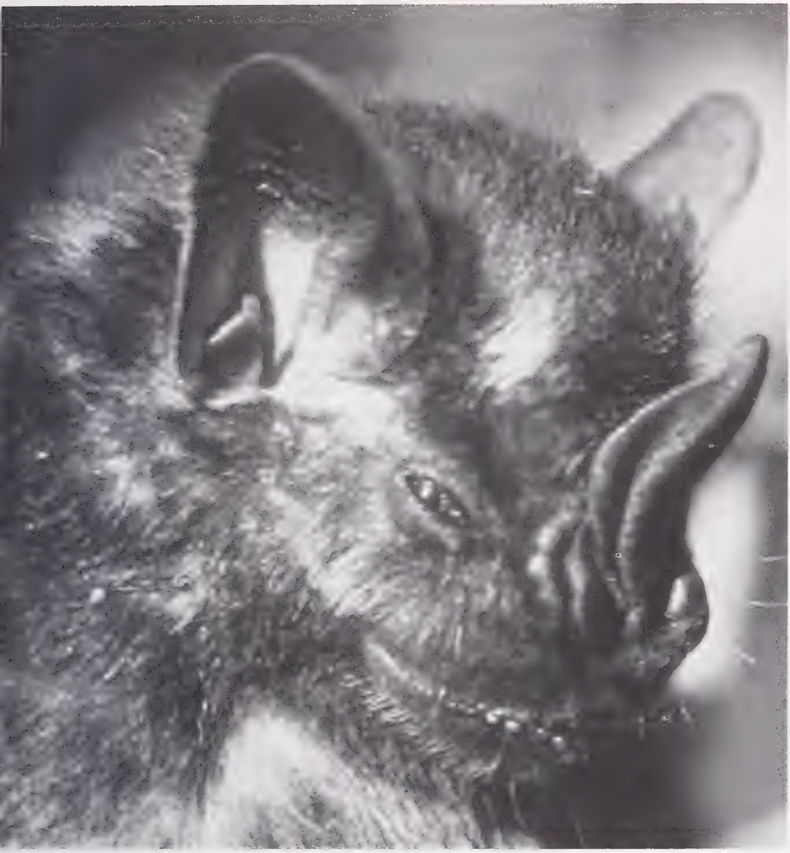


Fig. 55. Lowland fruit-eating bat, *Dermanura tolteca. Photo by R. K. LaVal.*

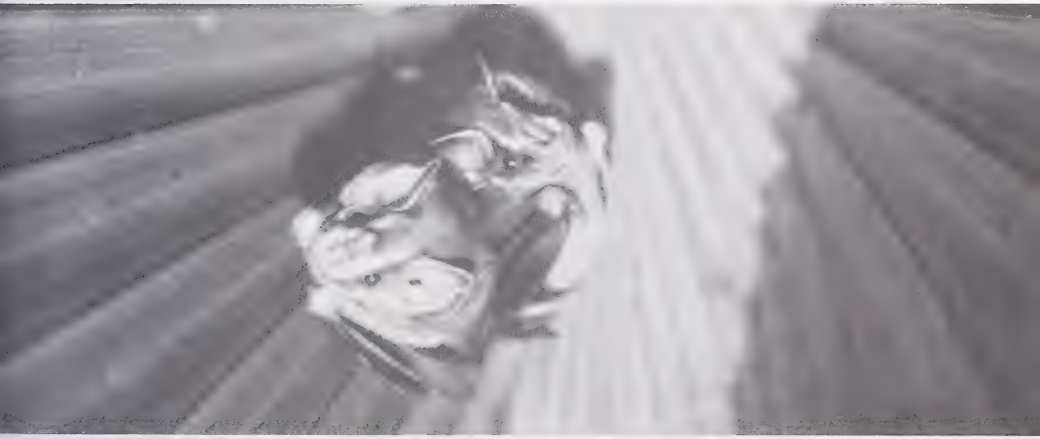


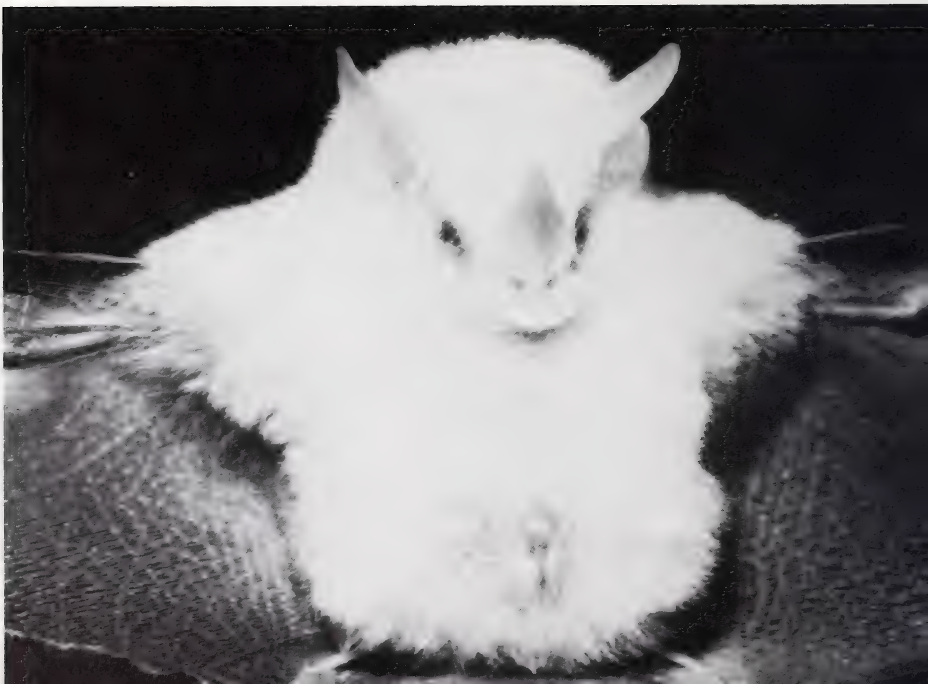
Fig. 56. Thomas' fruit-eating bat, *Dermanura watsoni. Photo by B. L. Clauson.*

Ectophylla alba
Caribbean White Bat

Caribbean white bats occur only from Honduras to Panama (Fig. 57). *Ectophylla alba* is a monotypic species.

White bats are limited to the Caribbean lowlands of Central America, where they occur in primary and old second-growth forests interspersed with *Heliconia* (Timm 1982). *Ectophylla* is one of the most distinctively colored bats; it is bright white with darker wings and bright orange-yellow ears and nose leaf. It is one of the few species of bats that actively alters the shape of leaves to create diurnal roosting sites. *Ectophylla* severs the side nerves and interconnected tissues on both *Heliconia* and *Calathea* from near the base to near the tip of the leaf causing the sides of the leaf to droop (Brooke 1987b; Timm 1982; Timm and Mortimer 1976). The roosting bats hang from the midrib of the leaf and are protected from predators and weather by their roosting structure, which has been termed a "tent." Brooke (1987b) reported that occupied tents typically contained four to eight roosting bats and that some tents were used only as night feeding roosts and others only as diurnal roosts. She found the birth of young to be highly synchronous, occurring in the latter half of April. *Ectophylla alba* is frugivorous; Brooke found fruit pulp and seeds from the small understory fig, *Ficus columbrinae*, under noctural feeding roosts. Several additional aspects of the biology of *E. alba* have been investigated at La Selva (Brooke 1987b; Greenbaum et al. 1975; LaVal and Fitch 1977; Timm 1982). The species is now known from a total of 12 localities, but only those at La Selva and the adjoining Braulio Carrillo and at Parque Nacional Tortuguero are in reserves where there is assurance that their habitat will be protected.

Fig. 57. Caribbean white bat, *Ectophylla alba. Photo by B. L. Clauson.*



Allen (1892) described the species based on a specimen he thought was from Honduras, but which actually was from Nicaragua. Later (1898) he described a subsequent specimen he thought was from Nicaragua, but which turned out to be from Costa Rica. Casebeer et al. (1963) finally collected three specimens unequivocally from La Selva. We have since observed them there regularly, and LaVal and Fitch (1977) reported capturing 38. Our specimens from Parque Nacional Braulio Carrillo were taken over a small stream in primary forest. One of the two females captured on 9 February 1983 was pregnant, carrying an embryo 7 mm in length.

Specimens examined (17)—Puerto Viejo, 100 m [1 female, KU]; 2.5 km SE of Puerto Viejo [1 female, CM]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 females, KU; 4 females, LACM; 5 males, MSB; 1 male, UMMZ; 1 female, USNM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, UNA; 1 female, USNM].

Sturnira lilium
Yellow-shouldered Bat

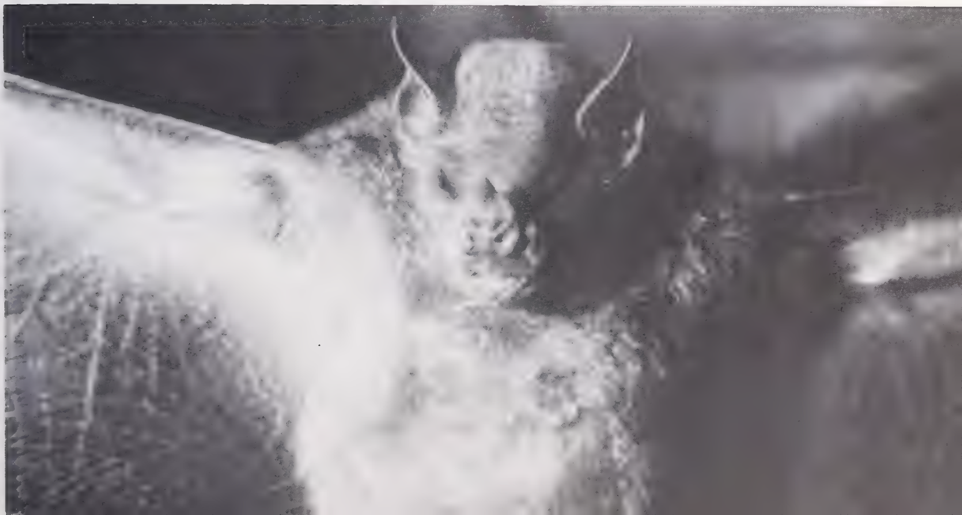
Yellow-shouldered bats are known from Sonora and Tamaulipas, Mexico, to Argentina (Fig. 58). The Costa Rican subspecies, *Sturnira lilium parvidens*, is found throughout Central America and Mexico.

An occupant of both dry and wet forests, this species is locally abundant throughout tropical lowlands. Roost sites include caves, tunnels, hollow trees, buildings, in culverts, and under bridges (Villa-R. 1967). Basically frugivorous, they also may feed occasionally on pollen or nectar (Gardner 1977). They are bimodally polyestrous in Costa Rica (Wilson 1979).

Mares and Wilson (1971) recorded 32 specimens from Guanacaste. Curiously, this species has never been taken at La Selva, although there is a single record from Puerto Viejo.

Specimen examined (1)—Puerto Viejo, Río Sarapiquí, 300 ft [1 female, UMMZ].

Fig. 58. Yellow-shouldered bat, *Sturnira lilium. Photo by B. L. Clauson.*



Sturnira ludovici
Anthony's Bat

Anthony's bats are widely distributed from Sinaloa and Tamaulipas, Mexico, to Peru and Bolivia (Fig. 59). The nominate subspecies, *Sturnira ludovici ludovici*, is found throughout Central America (de la Torre 1961). The systematic status of this species is not well understood; it is almost surely a composite as currently recognized in the literature. True *S. ludovici* probably are restricted to northern South America. The Central American bats under discussion here may prove to be a distinct species, for which the name *S. hondurensis* (Goodwin 1940) is available.

Although Anthony's bat inhabits a variety of forest types, it is frequently more common at intermediate elevations. Nothing is known about roosting sites. At Monteverde, Dinerstein (1986) found *S. ludovici* feeding on the fruits of 29 species of plants. The reproductive cycle is the familiar one of bimodal polyestry (Wilson 1979).

Goodwin (1946) reported two specimens from Agua Buena, Puntarenas Province. Starrett and de la Torre (1964) added one from Volcán Turrialba, Cartago Province. Mares and Wilson (1971) reported two from near San Vito de Java, Puntarenas Province. LaVal and Fitch (1977) caught one at La Selva. We found them to be fairly common at middle and higher elevations in Braulio Carrillo. Three of the females we caught in April were pregnant.

Specimens examined (11)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, UNA]; 1 km S, 11.5 km E of San Miguel, 680 m [3 females, USNM; 2 males, 1 female, USNM]; 5 km E of Vara Blanca, 2,050 m [2 females, USNM]; 2 km N, 0.5 km E of Sacramento, 2,600 m [1 female, FMNH].

Additional records (3)—3 mi N of Heredia, 5,600 ft [3 females, TCWC].

Sturnira luisi
Luis' Bat

Previously confused with *Sturnira lilium*, Luis' bat was recognized only recently as a distinct species (Davis 1980). The type locality for *S. luisi* is Cariblanco in Alajuela Province, Costa Rica, and it is now known to occur from Costa Rica to Peru.

Our specimens came from wet forest, and the distribution of the known specimens suggest this as the primary habitat. Nothing is known about the natural history of these bats due to their confusion with *S. lilium*. Presumably they are frugivorous like their congeners. None of our specimens evidenced any reproductive activity. Our specimens all came from over a small stream through pasture land in an otherwise primary forest zone. Paratypes are known from Limón Province, so finding them in the park is not surprising.

Specimens examined (4)—1 km S, 11.5 km E of San Miguel, 680 m [1 male, 2 females, USNM; 1 female, UNA].

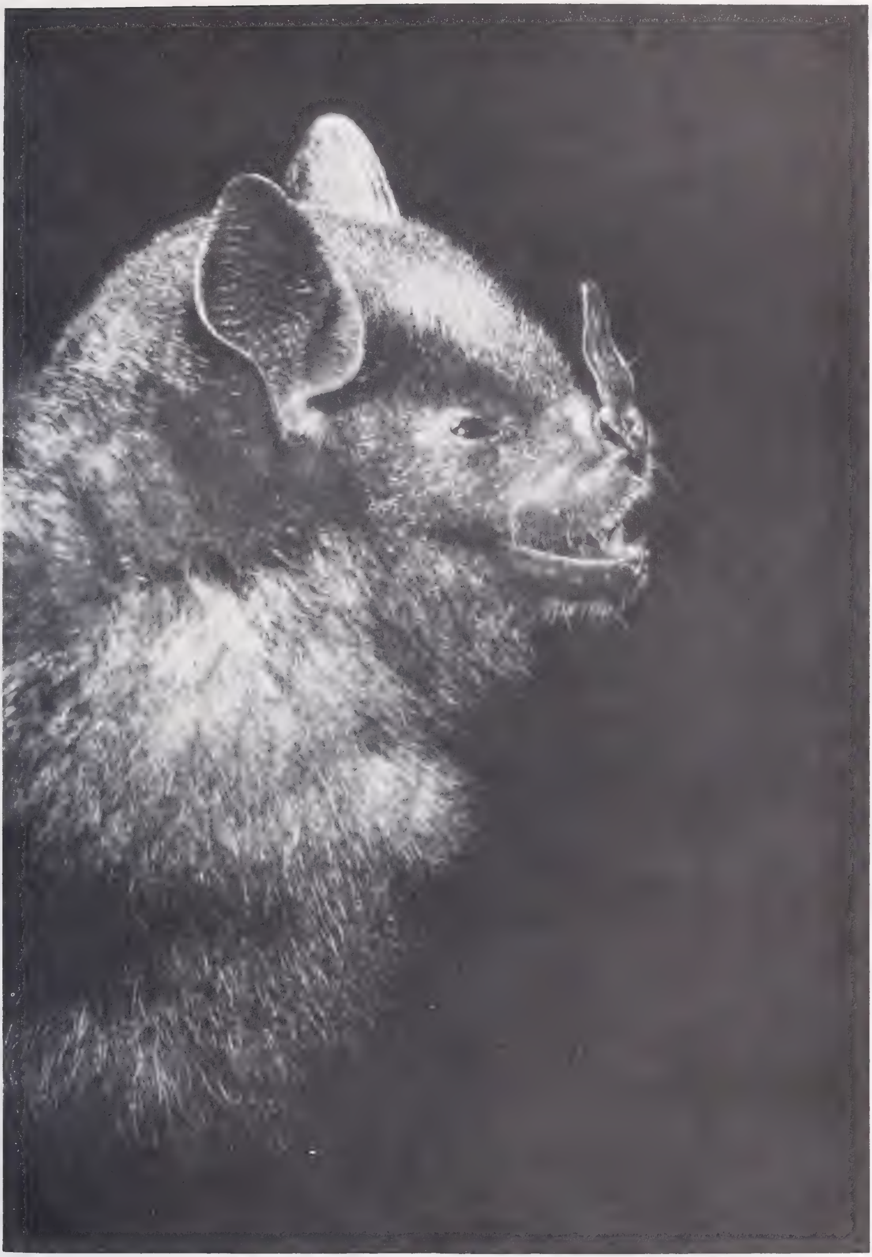


Fig. 59. Anthony's bat, *Sturnira ludovici. Photo by B. L. Clauson.*

Sturnira mordax
Talamancan Bat

Talamancan bats are endemic to the highlands of Costa Rica and adjacent western Panama (Fig. 60). The species is monotypic.

This is a middle to high elevation bat, found in both tropical and cloud forests. Roosting sites are unknown. They are frugivorous, and Howell and Burch (1974) reported the remains of four species of fruits in stomach contents. The reproductive cycle is polyestrous, probably bimodal based on the little data that are available and the fact that other species of *Sturnira* are bimodally polyestrous (Wilson 1979).

The type specimen was collected by C. Underwood at El Sauce Peralta, Costa Rica, in 1931. Davis et al. (1964) reported nine more from Cariblanco in Alajuela Province. Armstrong (1969) added a specimen from Finca Las Cruces near San Vito de Java, Puntarenas Province, and Gardner et al. (1970) added numerous specimens from several other localities. LaVal and Fitch (1977) found them at Monteverde. We found them to be common in Parque Nacional Braulio Carrillo from 700 to 2,000 m. We caught them in primary forest and along pasture edges. Two females were pregnant in April. Gardner et al. (1970) reported that an adult female they captured on 2 May at Vara Blanca was lactating. We obtained two species of bat flies, both are undescribed species, from *S. mordax*: *Megistopoda* sp. (10 males, 5 females) and *Trichobius* sp. (2 males).

Specimens examined (16)—1 km S, 11.5 km E of San Miguel, 680 m [2 males, 5 females, USNM]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [1 male, 3 females, USNM]; 9 km S, 11.5 km E of San Miguel, 1,520 m [1 male, USNM]; Vara Blanca [2 females, LSUMZ]; 5 km E of Vara Blanca, 2,050 m [1 male, 1 female, USNM].

Uroderma bilobatum
Tent-making Bat

Tent-making bats are found from Oaxaca and Veracruz, Mexico, to Brazil (Fig. 61). Two subspecies occur in Costa Rica: *Uroderma bilobatum molaris* on the Caribbean versant and *U. b. convexum* on the Pacific side.

This species is found in a wide variety of habitats ranging from primary humid and dry forests to second-growth forest and pasture. As the name implies, roosts are constructed by modifying large leaves to form a tent. The diet is mainly fruit, although pollen, nectar, and insects occasionally are taken. The reproductive pattern is one of bimodal polyestry (Wilson 1979). The biology of tent-making bats was summarized by Baker and Clark (1987).

Mares and Wilson (1971) reported *U. bilobatum* from a variety of localities in Costa Rica, including La Selva. LaVal and Fitch (1977) captured 17 at La Selva and noted that pregnant females were observed in January and February.

Specimens examined (17)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, FMNH; 2 males, LACM; 1 male, 1 female, MSB]; Puerto Viejo, Río Sarapiquí, 300 ft [2 males, UMMZ]; 7.3 mi SE of Puerto Viejo [1 female, TTU]; 8 mi SE of Puerto Viejo [2 males, 7 females, TTU].

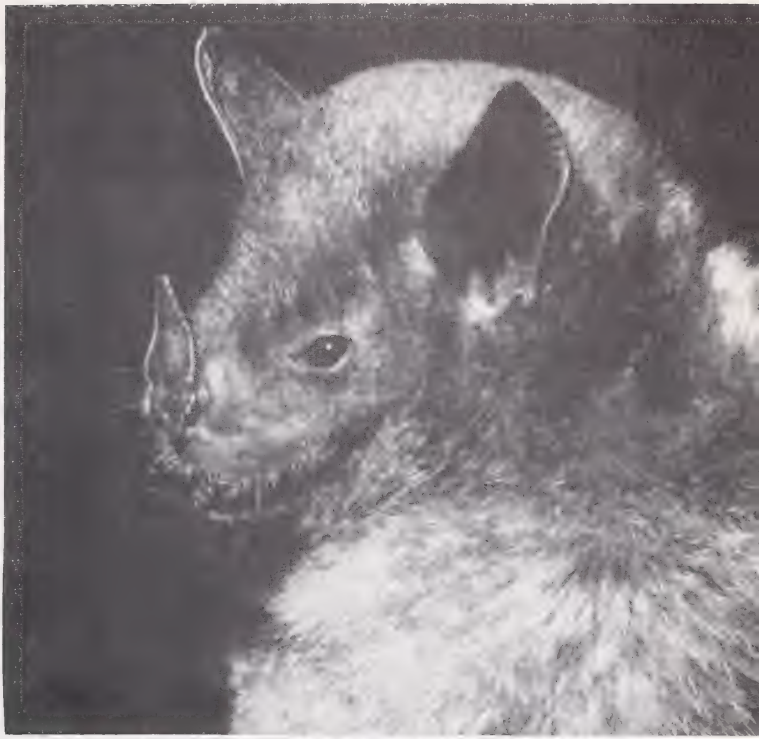


Fig. 60. Talamancan bat, *Sturnira mordax. Photo by B. L. Clauson.*

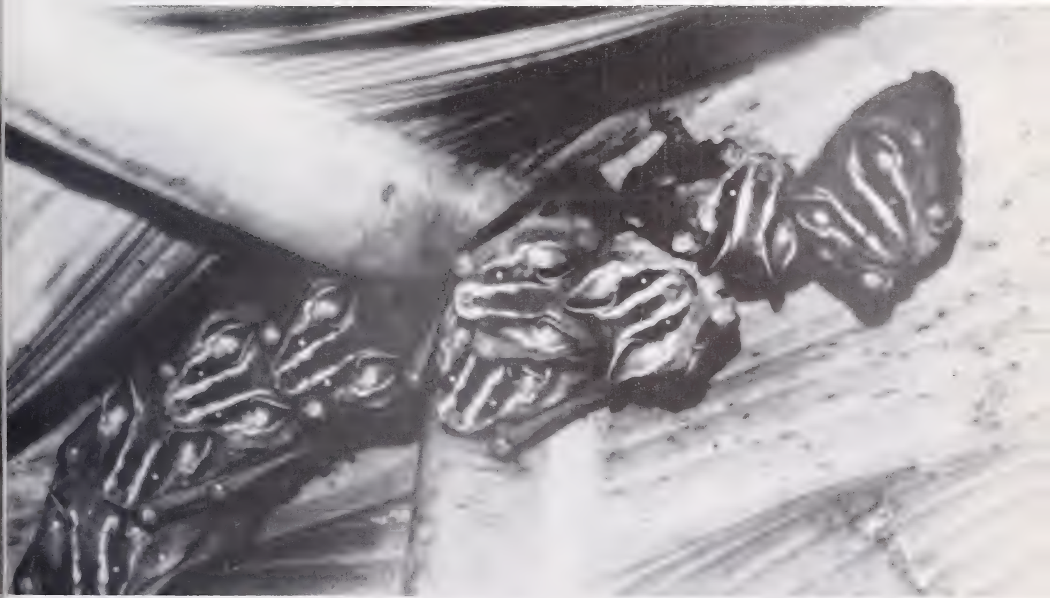


Fig. 61. Tent-making bats, *Uroderma bilobatum. Photo by R. M. Timm.*

Vampyressa nymphaea
Big Yellow-eared Bat

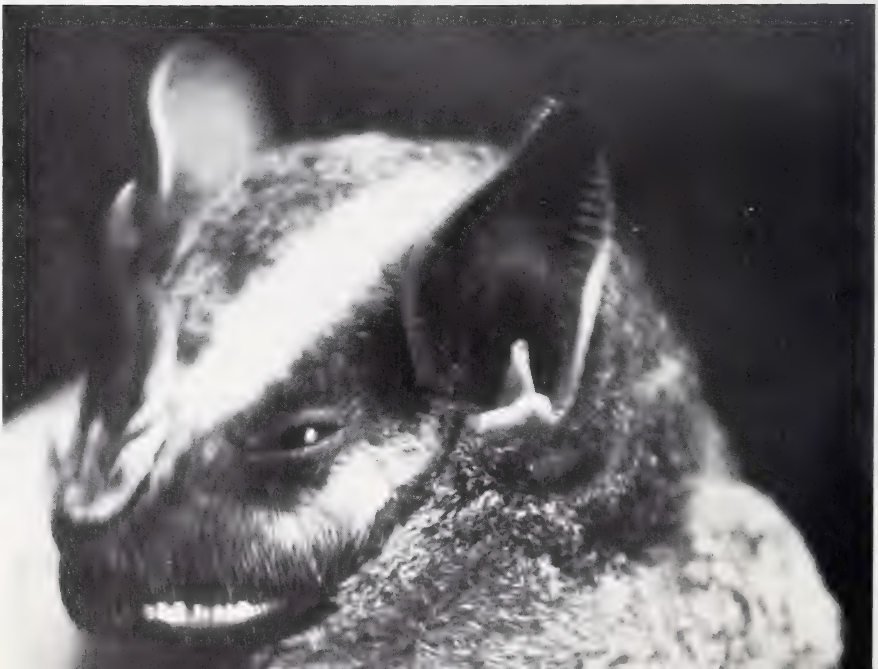
Big yellow-eared bats are found from Nicaragua through Costa Rica and Panama to Amazonian Brazil (Fig. 62). The species is monotypic.

This species is normally found in primary forest habitats. Although mainly frugivorous, some insect consumption has been reported (Fleming et al. 1972). The reproductive pattern is bimodal polyestry (Wilson 1979). Brooke (1987a), in a study of roosting ecology and social behavior of *Vampyressa nymphaea* at La Selva, found that these bats roosted exclusively under cut leaves of the understory shrub *Pentagonia donnell-smithii* (Rubiaceae). The bats severed the basal lateral nerves and the midrib near its midpoint to form a three-sided tent. One to three adult females roosted together with a single adult breeding male, suggesting a harem mating system. Pregnant females were found from early through mid-April. Tents were used for several days in succession, and there was some movement of individuals between tents. One tent was in use for more than 9 months, although not continuously (Brooke 1987a).

Gardner et al. (1970) reported the first *V. nymphaea* for Costa Rica from Cariari. Mares and Wilson (1971) reported additional specimens from Guanacaste and Puntarenas Provinces. LaVal and Fitch (1977) reported two from La Selva. Our specimen from Parque Nacional Braulio Carrillo was netted over a small stream with a closed canopy of riparian vegetation.

Specimens examined (3)—2.5 km SE of Puerto Viejo [1 male, CM]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, FMNH]; 1 km S, 11.5 km E of San Miguel, 580 m [1 male, USNM].

Fig. 62. Big yellow-eared bat, *Vampyressa nymphaea. Photo by R. K. LaVal.*



Vampyressa pusilla
Little Yellow-eared Bat

Little yellow-eared bats are found from Oaxaca and Veracruz, Mexico, to Brazil and Paraguay (Fig. 63). The Costa Rican subspecies, *Vampyressa pusilla thyone*, is found throughout Central America.

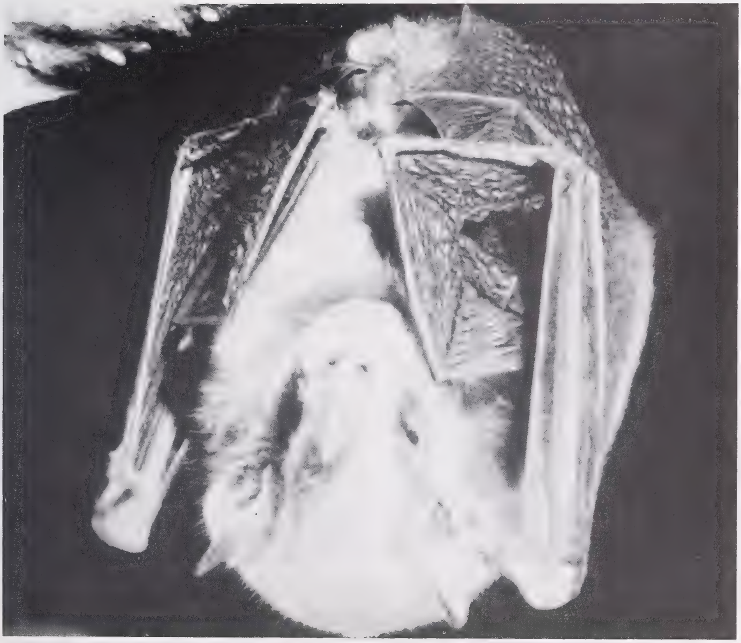
This species is found mainly in primary forest habitats, both wet and dry. Basically frugivorous, it has been reported to feed on *Acnistes* sp. in Costa Rica (Howell and Burch 1974). The reproductive cycle is the usual bimodal polyestry (Wilson 1979). Timm (1984) described the first known tent of little yellow-eared bats, which he found at La Selva. This species cuts the basal nerves of *Philodendron* leaves such that the sides of the leaf roll downward to form a pyramid-shaped tent. Brooke (1987b) found 128 *V. pusilla* tents in *Philodendron* at La Selva over a several month period; seven of the tents were occupied, most by single bats. Biology of *V. pusilla* was summarized by Lewis and Wilson (1987).

Goodwin (1946) reported the first Costa Rican specimens from Agua Buena, Puntarenas Province. Armstrong (1969) reported on specimens from the Osa Peninsula, and on one collected in 1961 at La Selva. LaVal and Fitch (1977) captured 27 at La Selva and noted that pregnant females were seen in February, April, July, August, and September. A flightless juvenile was collected at La Selva on 17 July 1974.

Specimens examined (7)—Cariblanco [1 female, KU]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, FMNH; 1 male, 1 female, KU; 2 males, 1 sex ?, MSB].

Additional record (1)—1.5 mi S of Cariblanco [1 male, MVZ].

Fig. 63. Little yellow-eared bat, *Vampyressa pusilla. Photo by R. K. LaVal.*



Vampyrodes caraccioli
San Pablo Bat

San Pablo bats are known from Oaxaca and southern Veracruz, Mexico, to Brazil and Bolivia (Fig. 64). The Costa Rican subspecies, *Vampyrodes caraccioli major*, is considered by some to be a species (*V. major*) distinct from the South American *V. caraccioli*.

This species is found predominately in primary forest habitats and is more common in low to middle elevation wet forests. The bats roost in small groups in foliage (Tuttle 1976). The diet is restricted to fruit (Gardner 1977). The reproductive pattern is bimodal polyestry (Wilson 1979).

The first specimen from Costa Rica was reported by Goldman (1920) from Alajuela Province. Starrett and Casebeer (1968) added several more from various localities. LaVal and Fitch (1977) took a single pregnant female from La Selva in February.

Specimens examined (22)—Puerto Viejo, 100 m [1 male, KU]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 sex ?, MSB]; 7.3 mi SE of Puerto Viejo [11 males, 9 females, TTU].

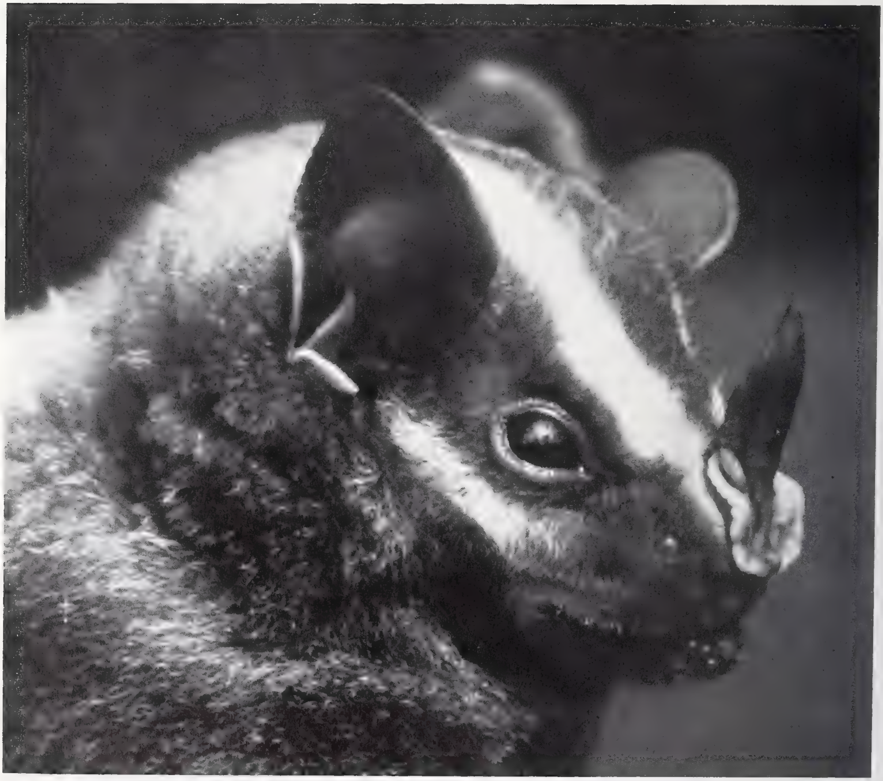


Fig. 64. San Pablo bat, *Vampyrodes caraccioli. Photo by R. K. LaVal.*

Vampyrops helleri
Heller's Broad-nosed Bat

Heller's broad-nosed bats occur from Oaxaca and Veracruz, Mexico, to central Brazil (Fig. 65). If subspecies are recognized in *Vampyrops helleri*, the nominate form occurs throughout Central America.

This species is found in primary forest habitats and occasionally in second-growth and riparian situations. Roost sites include caves, tunnels, buildings, culverts, and bridges, as well as foliage (Tuttle 1976). Although essentially frugivorous, this species occasionally takes insects (Howell and Burch 1974). Data on reproduction are too few to suggest a definitive pattern (Wilson 1979).

Goodwin (1946) reported a specimen from Jiménez, Limón Province. Mares and Wilson (1971) added specimens from the Osa Peninsula and San Vito, Puntarenas Province. LaVal and Fitch (1977) reported 17 from La Selva; their only pregnant female was found in August. We took two males in Parque Nacional Braulio Carrillo, both from primary forest on a well-drained ridge.

Specimens examined (9)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [2 females, KU; 3 males, 2 females, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, USNM; 1 male, UNA].

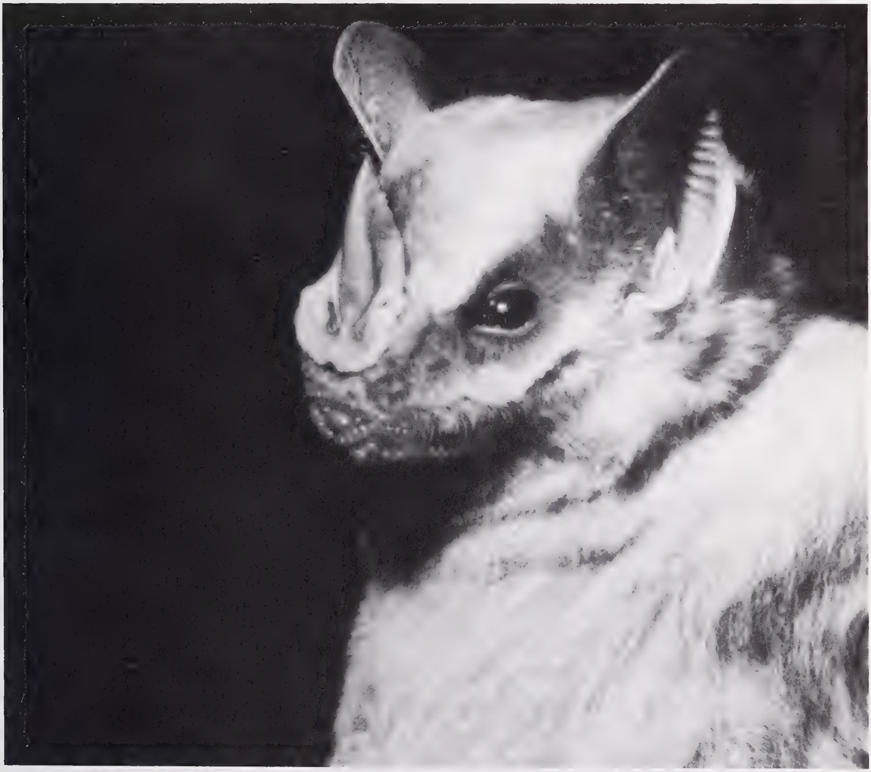


Fig. 65. Heller's broad-nosed bat, *Vampyrops helleri. Photo by B. L. Clauson.*

Vampyrops vittatus
Greater Broad-nosed Bat

Greater broad-nosed bats reach their northern limit in Costa Rica, and extend as far south as Bolivia (Fig. 66). *Vampyrops vittatus* is a monotypic species.

This broad-nosed bat is most common at intermediate elevations in wet and moist forest habitats (Handley 1976). Roosting sites have been reported from caves and tunnels, overhanging roots, and under stream banks (Tuttle 1976). Gardner (1977) listed this species as frugivorous. Little is known about the reproductive pattern, but the species is presumed to be bimodally polyestrous (Wilson 1979).

Dobson (1878) first reported *V. vittatus* from Costa Rica (undesignated locality), and Tamsitt and Valdivieso (1961) reported a second specimen from San José. Davis et al. (1964) collected 9 specimens from Cariblanco, Alajuela Province, and Gardner et al. (1970) reported 16 from Vara Blanca, Heredia Province.

Specimens examined (16)—Vara Blanca [6 males, 10 females, LSUMZ].

Subfamily Desmodontinae

Desmodus rotundus
Common Vampire Bat, Vampiro

Common vampires occur from Sonora and Tamaulipas, Mexico, to Argentina (Fig. 67). The Costa Rican subspecies, *Desmodus rotundus murinus*, occurs throughout Mexico and Central America.

Common vampires have adapted to a wide variety of habitats and prosper where man has introduced livestock. They are much less common in primary forest. Roost sites include caves, tunnels, hollow trees, culverts, bridges, and rock crevices (Tuttle 1976). The diet is restricted to blood, primarily mammalian, although we have also observed them feeding on chickens. Reproduction is continuous, probably due to the artifically high food supply provided by domestic livestock. The biology of vampires was summarized by Greenhall et al. (1983) and Greenhall and Schmidt (1988). Turner (1975, 1983) summarized natural history information for Costa Rica.

In a several-month study of vampires at La Selva, Young (1971) reported a colony of 40 to 47 individuals in the hollow of a large *Ceiba pentandra* tree, while a second colony of 54 to 68 individuals roosted between two gnarled buttresses of a giant *Terminalia bucidoides* tree (Combretaceae). One roost site also contained a colony of greater white-lined bats (*Saccopteryx bilineata*), but there was little to no interaction between the vampires and sac-winged bats. Young noted a high degree of site fidelity in the vampires. The individuals he observed typically fed on cattle located 2.4 km from the roosting sites. Although he found reproduction concentrated in a 2 month period (March through April), investigators in other areas have found vampires to breed the year around.

Goodwin (1946) reported specimens from Cartago Province. Mares and Wilson (1971) reported vampires from Guanacaste Province and also seven specimens from La Selva. LaVal and Fitch added 29 from La Selva. Our specimens from Braulio Carrillo came from forested areas near old pastures.

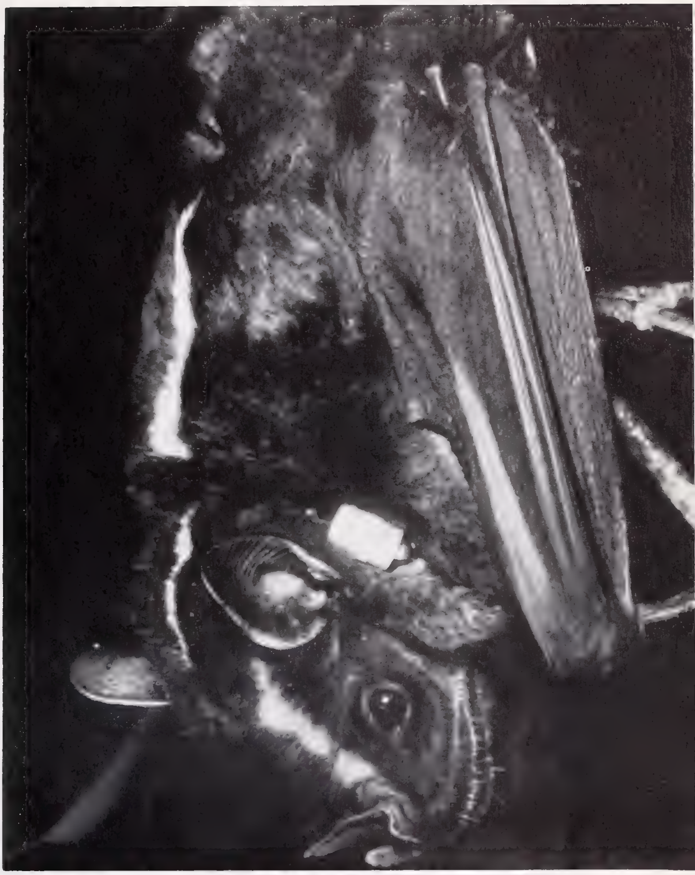


Fig. 66. Greater broad-nosed bat, *Vampyrops vittatus. Photo by R. K. LaVal.*

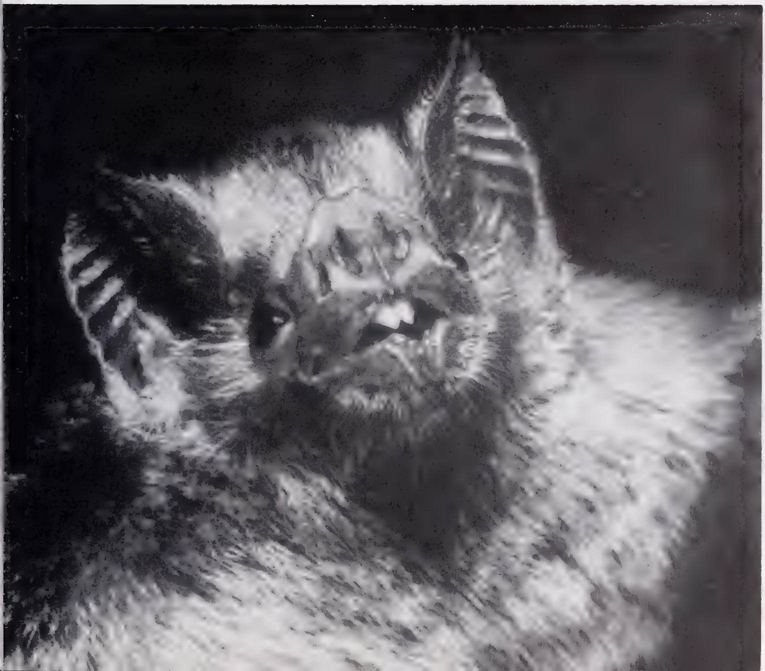


Fig. 67. Vampire bat, *Desmodus rotundus. Photo by B. L. Clauson.*

Parasitic streblid bat flies we found on vampire bats include *Strebla wiedemanni* (1 female) and *Trichobius parasiticus* (1 male, 1 female).

Specimens examined (7)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM]; 1 km S, 11.5 km E of San Miguel, 580 m [3 females, USNM; 1 male, UNA]; 5 km E of Vara Blanca, 2,050 m [1 female, USNM].

Additional records (2)—4 mi W of Puerto Viejo, 300 ft [1 female, TCWC]; Vara Blanca [LSUMZ; Gardner et al. 1970].

Family Furipteridae

Furipterus horrens
Smoky Bat

Smoky bats reach the northern limit of their range in Costa Rica and are known from South America as far south as Brazil. *Furipterus horrens* is a monotypic genus and species.

Although this species is primarily restricted to mesic forest habitats, it has been reported from dry forest in South America (Uieda et al. 1980). Roost sites are in caves, hollow logs, and rock crevices (LaVal 1977; Uieda et al. 1980). Uieda et al. (1980) reported moths to be important dietary items. Scattered reports of reproductive activity are insufficient to speculate on the annual cycle.

LaVal (1977) found a roost in a hollow log at La Selva containing more than 59 individuals. This is the northernmost locality for the species, and the only known Costa Rican locality of record.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, 1 female, KU].

Family Thyropteridae

Thyroptera tricolor
Spix's Disk-winged Bat

Spix's disk-winged bats are known from Veracruz, Mexico, to southern Brazil (Fig. 68). The Costa Rican subspecies, *Thyroptera tricolor albiventer*, occurs throughout Central America. Disk-winged bats occur from sea level to middle elevations.

This species is found in wet forest habitats with stands of *Heliconia* spp. Individuals roost inside the tubular emerging leaves of these plants and also of the introduced banana (*Musa sapientum*), holding onto the leaf with the unique suction cups on their wrists and ankles (Findley and Wilson 1974). They are insectivorous, but details of the diet are unknown. They roost in family groups, but details of the reproductive cycle are not available (Wilson and Findley 1977).

Goodwin (1946) reported the first Costa Rican specimens from Puntarenas Province. Starrett and de la Torre (1964) added a specimen from Golfito, and Gardner et al. (1970) also reported *Thyroptera tricolor* from the Osa Peninsula. Our specimen from Parque Nacional Braulio Carrillo was captured in a mist net across a narrow road through an old pasture, with primary forest nearby. Disk-winged bats have been observed at La Selva on only a few occasions. The specimen now at LACM was taken in the early 1960's and was the first from the Caribbean

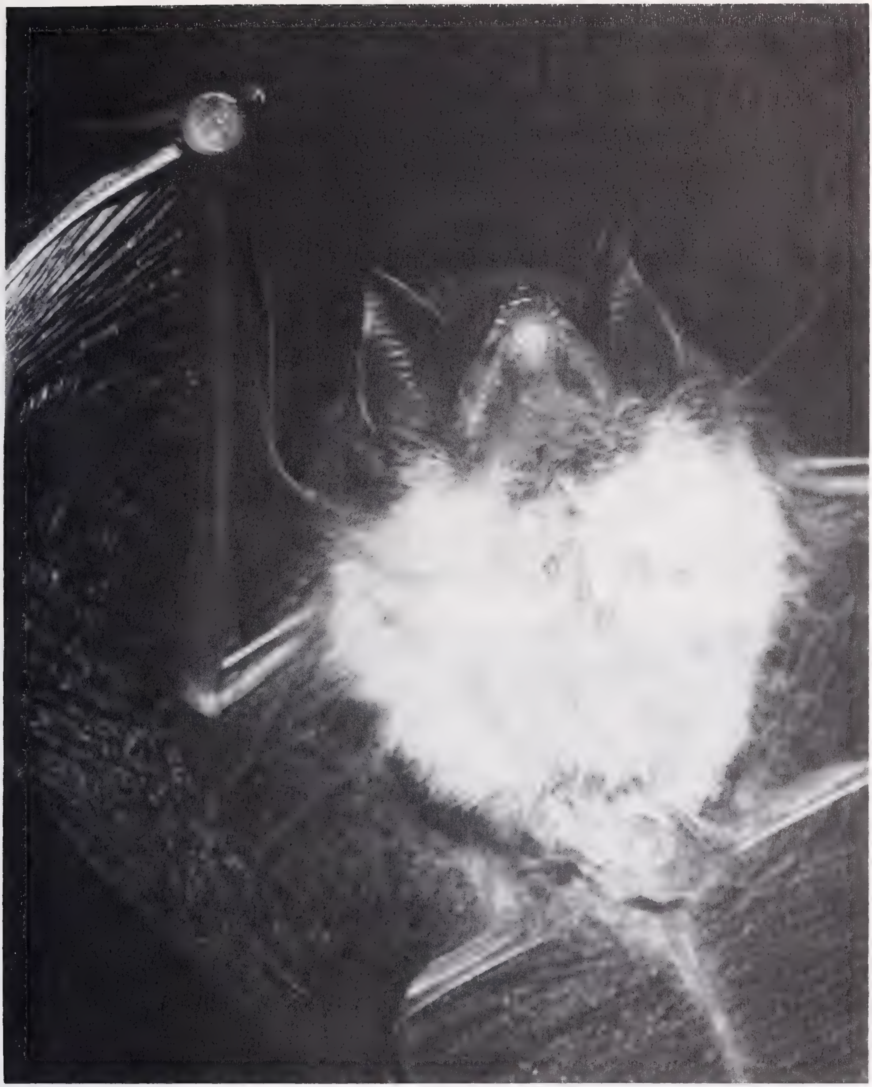


Fig. 68. Spix's disk-winged bat, *Thyroptera tricolor. Photo by B. L. Clauson.*

lowlands of Costa Rica. A single individual was recorded in the mammal log at La Selva on 23 May 1983. In June 1988, a colony of seven disk-winged bats was found in an unfurled *Heliconia* leaf near the field station at La Selva, and another colony was found in the same area in May 1989. *Thyroptera* is common in other lowland areas in Costa Rica. It is abundant at Tortuguero and on the Osa Peninsula, but may be locally restricted to areas that combine *Heliconia* stands with substantial canopy cover.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo [1 male, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM].

Family Vespertilionidae

Eptesicus brasiliensis
Brazilian Brown Bat

Brazilian brown bats are found from Veracruz, Mexico, to Argentina (Fig. 69). The Costa Rican subspecies, *Eptesicus brasiliensis andinus*, occurs in the highlands of Central America. It may warrant recognition as a distinct species (*E. andinus*).

Although this species normally is found in highland areas in Central America, its presence at La Selva (LaVal and Fitch 1977) and at 270 m in the Zona argues for broader habitat tolerance. These bats frequently roost in buildings or in hollow trees (Handley 1976). They are insectivorous, but details of the diet are unknown. Reproductive records suggest the possibility of a polyestrous pattern.

This species has been taken at several localities in the highlands of Costa Rica (Starrett and Casebeer 1968). LaVal and Fitch (1977) captured one at La Selva. Our lowland specimen from Parque Nacional Braulio Carrillo was caught in a net placed over a small stream, and the highland specimen was netted in an old pasture near a small strip of riparian forest.

Specimens examined (2)—11.5 km S, 4.5 km W of Puerto Viejo, 270 m [1 female, USNM]; 5 km E of Vara Blanca, 2,050 m [1 male, USNM].

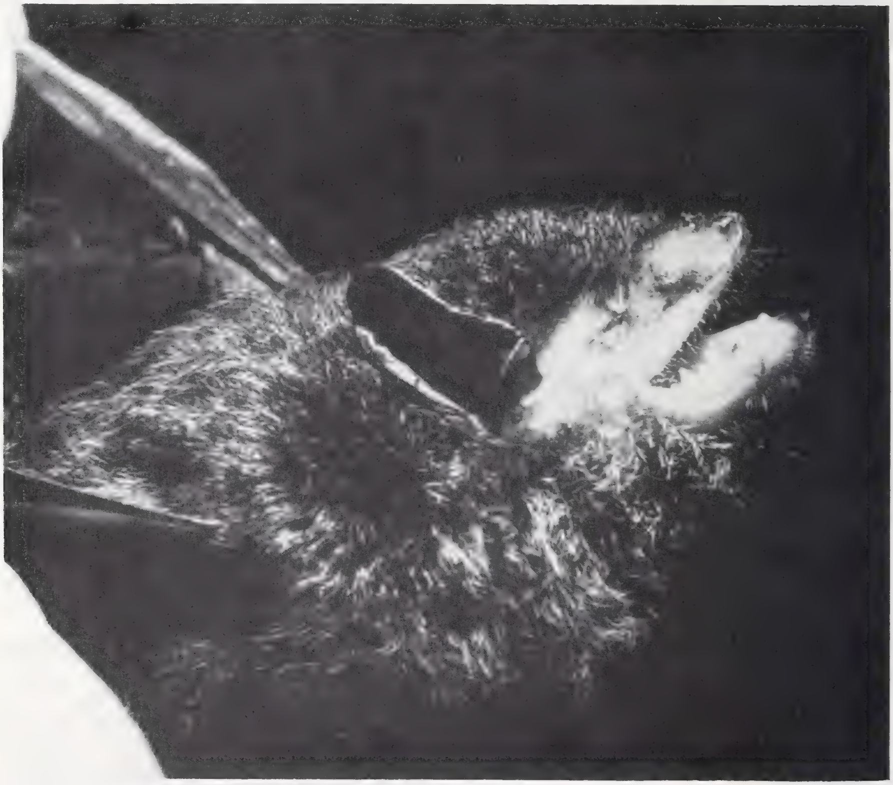


Fig. 69. Brazilian brown bat, *Eptesicus brasiliensis. Photo by B. L. Clauson.*

Eptesicus furinalis
Argentine Brown Bat

Argentine brown bats range from Jalisco and Tamaulipas, Mexico, south to Argentina. Davis (1965) considered Costa Rican animals to belong to a distinct subspecies, which he described as *Eptesicus gaumeri carteri*. Subsequently (Davis 1966), he arranged both *gaumeri* and *carteri* as subspecies of the wide-ranging *E. furinalis*. Additional study of geographic variation in this species is warranted.

This species occurs in a wide range of environmental conditions from sea level to high montane habitats. Roosts are known from caves, buildings, hollow trees, and logs (Villa-R. 1967). These bats are insectivorous, but details of the diet are unknown. The reproductive cycle has not been studied adequately in any given locality.

Starrett and Casebeer (1968) listed specimens from Puntarenas, Limón, and Alajuela Provinces. LaVal and Fitch (1977) captured a single individual from La Selva. Apparently no specimens have been preserved from this region.

Lasiurus ega
Southern Yellow Bat

Southern yellow bats are found from southeastern Texas and adjacent Mexico to Argentina. A single subspecies, *Lasiurus ega panamensis*, is known from Central America. Systematics of the genus *Lasiurus*, based on genic data, were reviewed recently by Baker et al. (1988).

This species has an enormous range, and has been taken in a wide variety of habitats ranging from xeric desert scrub to rainforest. These bats normally roost in foliage. Details of food habits are not known; however, the species is certainly insectivorous. These bats are monestrous; litter size varies from one to three (Nowak and Paradiso 1983).

Goodwin (1946) recorded this species from San José and Alajuela Provinces. Starrett and Casebeer (1968) added specimens from Puntarenas Province, and Gardner et al. (1970) recorded specimens from the Meseta Central. Our specimen is the first from the Caribbean slope of Costa Rica.

Specimen examined (1)—11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, USNM].

Myotis albescens
Silver-tipped Myotis

The silver-tipped myotis ranges from Chiapas, Tabasco, and Veracruz, Mexico, to Argentina. *Myotis albescens*, a monotypic species, is typical of lowland rain forests, although individuals were netted from as high as 1,500 m by LaVal (1973a).

These bats usually are found in areas of mature forest, although they also follow riparian corridors through disturbed habitats. They roost in caves, hollow trees, and buildings. They are strictly insectivorous. The reproductive cycle is one of seasonal polyestry (Myers 1977).

Goodwin first reported the species from Costa Rica based on a specimen from Guanacaste Province. Gardner et al. (1970) added a specimen from the Caribbean lowlands. LaVal (1977) found two roosting in a building at La Selva, and five, including three pregnant females, roosting with *Molossus sinaloae* in a building in Puerto Viejo in January. One species of bat fly, *Basilia costaricensis* (two females), was obtained on a single *M. albescens* at La Selva.

Specimens examined (3)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU; 1 male, LACM]; 1 km S, 11.5 km E of San Miguel, 270 m [1 female, USNM].

Myotis elegans
Elegant Myotis

The elegant myotis occurs from San Luis Potosí, Mexico, to Costa Rica (Fig. 70). The species is monotypic. *Myotis elegans* is among the smallest of the Neotropical myotis. It is a lowland species, typically found from sea level to 300 m, although it is known from as high as 750 m.

Most individuals have been taken in forested areas, both wet and dry. Roosts have not been described. This is an insectivorous species. Although occasional reproductively active individuals have been reported, nothing is known about the annual pattern.

This species reaches the known southern limit of its range in Costa Rica, where it is known only from the La Selva area and Guanacaste Province (LaVal 1973a, 1977). LaVal caught 20 at La Selva. An undescribed species of bat fly (Nycteribiidae) of the genus *Basilia* (1 male, 3 females) was collected on an elegant myotis at La Selva.

Specimens examined (2)—5.5 mi N, 1 mi E of Puerto Viejo, 120 m [1 female, TCWC]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU].

Myotis keaysi
Hairy-legged Myotis

Bats of this polytypic species are found from Tamaulipas, Mexico, throughout Central America except for most of Panama, then south in South America to Peru. The Costa Rican subspecies is *Myotis keaysi pilosatibialis*. In Central America as a whole, the elevational range of hairy-legged myotis is from sea level to more than 2,500 m. Interestingly, all lowland records of this species are from north of Honduras.

This bat has been taken in a variety of habitats ranging from arid scrub to tropical rain forest. Few roosts have been documented, but individuals use caves, hollow trees, and perhaps buildings in some areas. The species is definitely insectivorous. The reproductive cycle is seasonal polyestry (LaVal and Fitch 1977). Individuals captured near San Miguel were taken in mist nets in undisturbed primary forest.

LaVal (1973a) reported hairy-legged myotis from several localities in Costa Rica. All Costa Rican localities of record for *M. keaysi* seem to be from middle and high elevations. The specimens taken from Cinco Esquinas, Heredia Province, were part of a colony of 200 individuals that W. E. Duellman found roosting at night under a bridge.

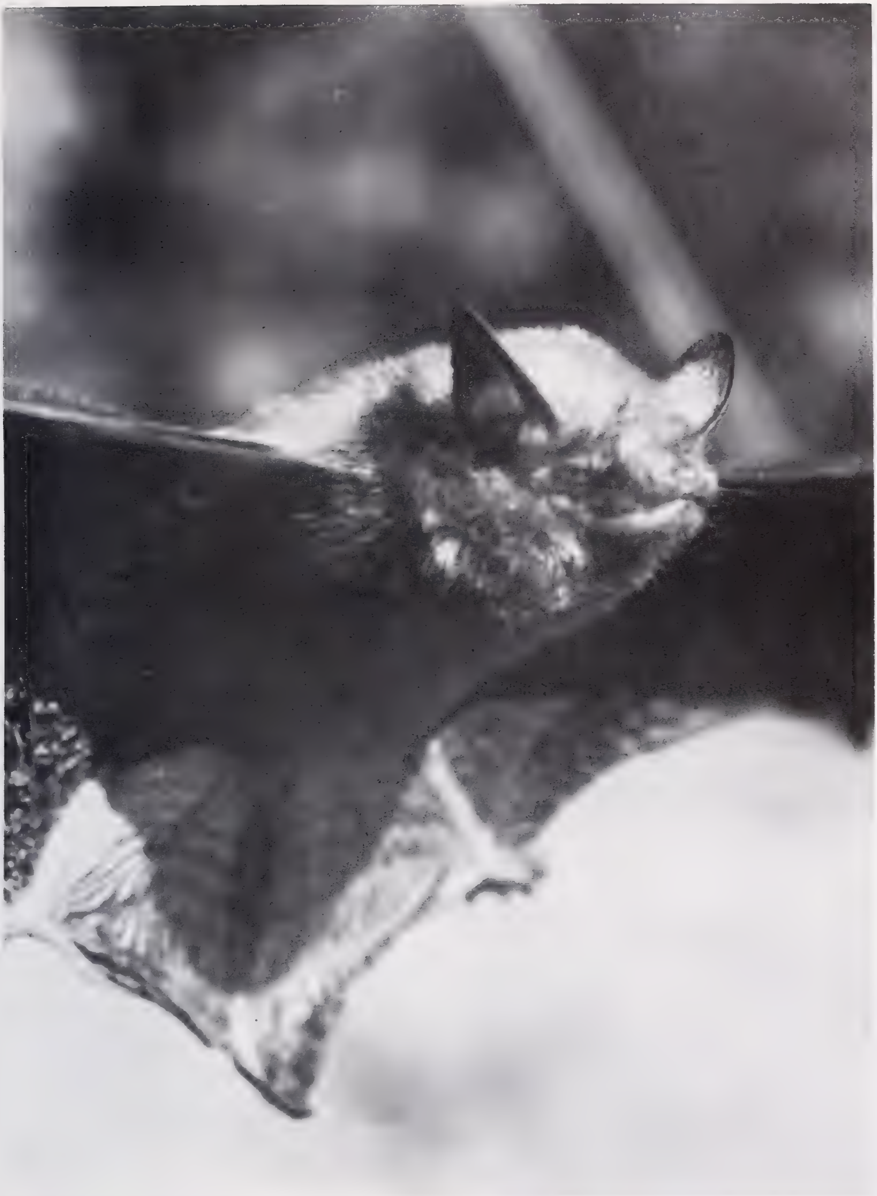


Fig. 70. Elegant myotis, *Myotis elegans. Photo by R. K. LaVal.*

Specimens examined (34)—2 km N of Cinco Esquinas, 1,550 m [21 males, 2 females, KU; 5 males, LACM]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [1 male, UNA; 2 males, USNM]; Vara Blanca, 1,800 m [1, LSUMZ]; Volcán Barva, 3.2 km S of Los Cartagos, ca. 1,800 m [2, LACM].

Myotis nigricans
Black Myotis

The black myotis is distributed from Tamaulipas, Mexico, to Argentina (Fig. 71). The nominate subspecies, *Myotis nigricans nigricans*, is found throughout Central America.

This species is known from almost all vegetation types within its broad range. In Costa Rica it is found from sea level to above 3,000 m. Black myotis roost in buildings, caves, tunnels, and hollow trees. The reproductive cycle is one of seasonal polyestry with a short diapause during the end of the rainy season (Wilson 1971b). The biology of black myotis was summarized by Wilson and LaVal (1974) and Wilson (1983b).

Goodwin (1946) reported black myotis from several Costa Rican localities, and subsequent workers have found this species occurring in most areas of the country. LaVal took 14 during his study at La Selva (LaVal and Fitch 1977). Our specimens from Parque Nacional Braulio Carrillo were caught in mist nets set over small streams near large tracts of primary forest. We obtained two species of bat flies on *M. nigricans*: *Anatrichobius scorzai* (1 female) and *Basilia* sp. (4 males, 3 females).

Specimens examined (19)—Puerto Viejo de Sarapiquí [2 males, 1 female, LACM]; Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 female, KU]; 5.7 mi S of Puerto Viejo [1 male, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 270 m [1 male, USNM]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, USNM]; Volcán Barva, 3.2 km S of Los Cartagos, ca. 1,800 m [12, LACM].

Myotis oxyotus
Montane Myotis

Montane myotis reach their northern limit in Costa Rica; the species extends south to Bolivia (Fig. 72). The Central American subspecies (LaVal 1973a) is *Myotis oxyotus gardneri*.

In Central America, the montane myotis is known only from highland areas of the Cordillera Talamanca in Panama and Costa Rica, and the Cordillera Tilaran of Costa Rica. The Vara Blanca specimen represents the northeasternmost record of the species. The habitat there is moist oak forests and cloud forests. We have also taken this species on several occasions in the Monteverde region. Montane myotis are insectivorous, but details of the food habits are unknown. The few records of reproductive activity (Gardner et al. 1970) suggest a monestrous cycle, with young born in summer.

The first Costa Rican records came from near Villa Mills on Cerro de la Muerte (Starrett and Casebeer 1968). Gardner et al. (1970) collected specimens from San José and Cartago Provinces in addition to the single male from Vara Blanca in Heredia Province.

Specimen examined (1)—Vara Blanca, 1,800 m [1 male, LSUMZ].

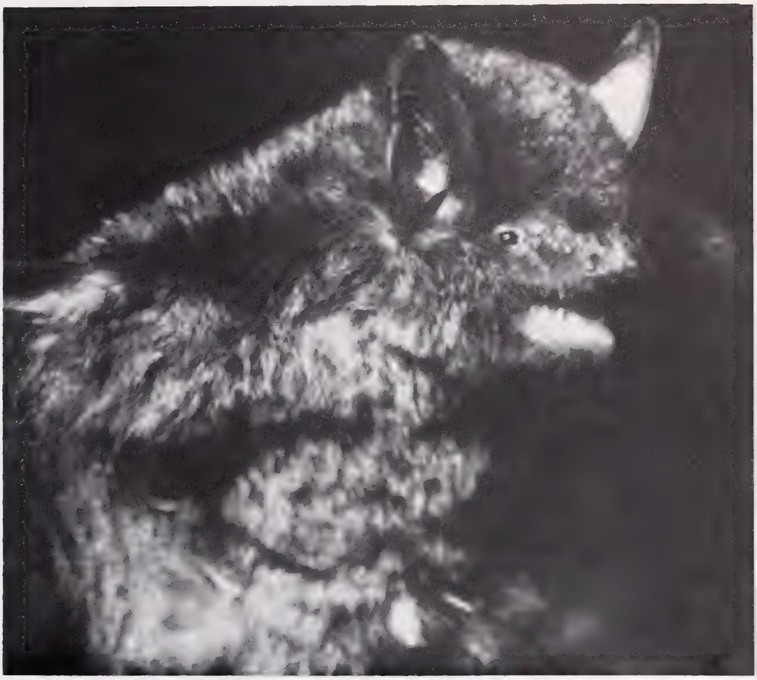


Fig. 71. Black myotis, *Myotis nigricans. Photo by B. L. Clauson.*

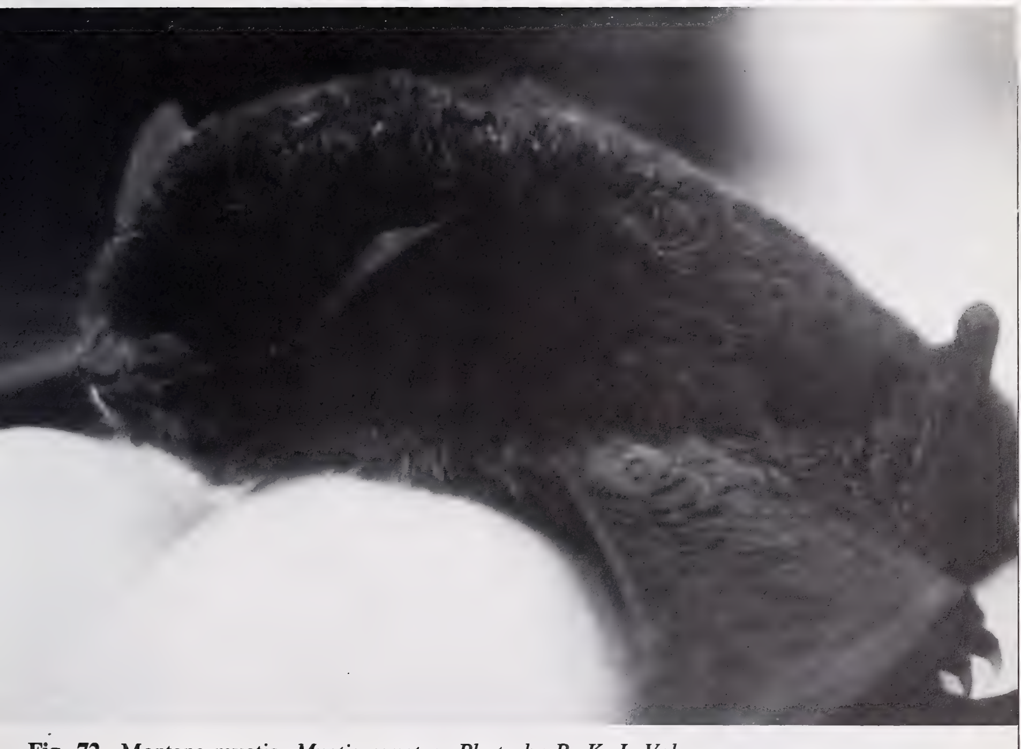


Fig. 72. Montane myotis, *Myotis oxyotus. Photo by R. K. LaVal.*

Myotis riparius
Riparian Myotis

Myotis riparius, a monotypic species, is found from Honduras to Uruguay. It occupies a wide elevational range, and habitats include both forested and savannah regions. Roosting sites are not known. Like other members of this genus, *Myotis riparius* are strictly insectivorous. At La Selva, the reproductive cycle is monestrous (LaVal and Fitch 1977).

LaVal (1973a) reported specimens from Limón and San José Provinces. He found the species common at La Selva, where he captured 78 (LaVal and Fitch 1977).

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo, 70 m [1 male, KU].

Rhogeessa tumida
Central American Yellow Bat

Central American yellow bats are found from Oaxaca and Tamaulipas, Mexico, to Brazil (Fig. 73). *Rhogeessa tumida* has been considered a monotypic species, although the degree of chromosomal and morphological variation present suggests that several biological species may be represented (LaVal 1973b).

Almost all types of habitats found within its range are occupied by *R. tumida*, which occurs from sea level to 1,500 m in Costa Rica (LaVal 1973b). They are known to roost in buildings (Goodwin 1946), and are insectivorous. Reproductive data suggest a limited breeding season, but are too few to understand the cycle.

The first record for Costa Rica was that of Sanborn (1932) from Guanacaste Province. Goodwin (1946) reported these specimens from Puntarenas Province. LaVal and Fitch (1977) captured one at La Selva. Our three specimens came from mist nets set across a small stream in primary forest.

Specimens examined (3)—11 km S, 4.5 km W of Puerto Viejo, 270 m [2 females, USNM; 1 female, UNA].

Family Molossidae

Molossus bondae
Bonda Mastiff Bat

Bonda mastiff bats are known from Honduras to Colombia, Ecuador, Venezuela, and Guyana (Fig. 74). The species is monotypic, and seems to be limited to forested regions in the Caribbean versant in the northern part of its range. Colonies commonly roost in buildings. The diet is made up completely of insects, which are taken on the wing. Little is known of reproduction, but pregnant females have been recorded in August and January in Costa Rica (LaVal 1977).

First reports of this species from Costa Rica were by Gardner et al. (1970), based on specimens from Cartago and Limón Provinces. LaVal (1977) reported a colony roosting under the roof of a building in Puerto Viejo. We captured and released an adult male and female at La Selva in June 1982. We mist-netted a single individual in Braulio Carrillo over a quiet pool in a small stream flowing through a recently cleared pasture.

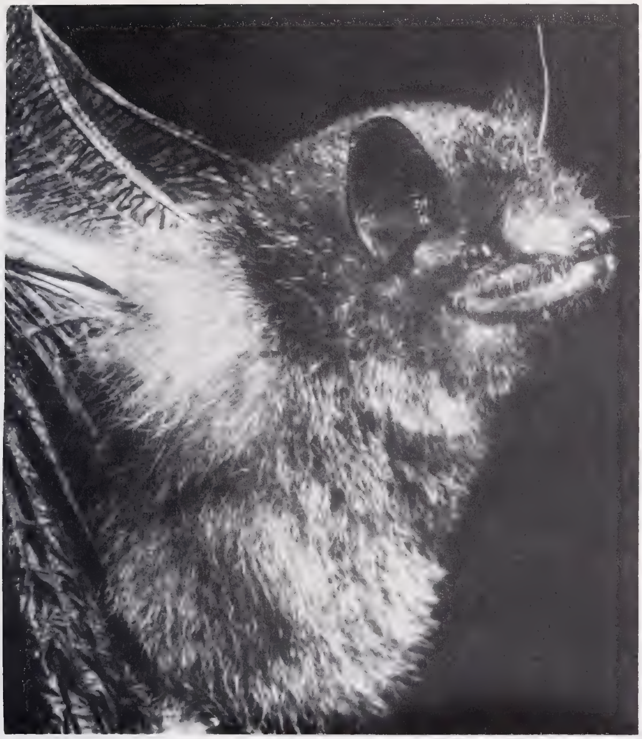


Fig. 73. Central American yellow bat, *Rhogeessa tumida. Photo by B. L. Clauson.*

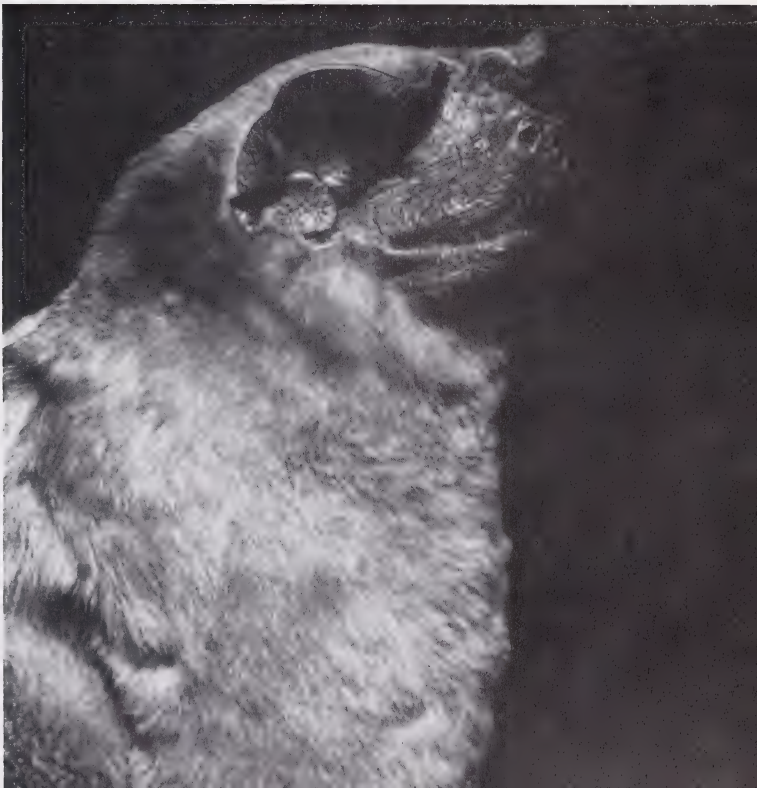


Fig. 74. Bonda mastiff bat, *Molossus bondae. Photo by B. L. Clauson.*

Specimen examined (1)—1 km S, 11.5 km E of San Miguel, 680 m [1 female, USNM].

Molossus sinaloae
Allen's Mastiff Bat

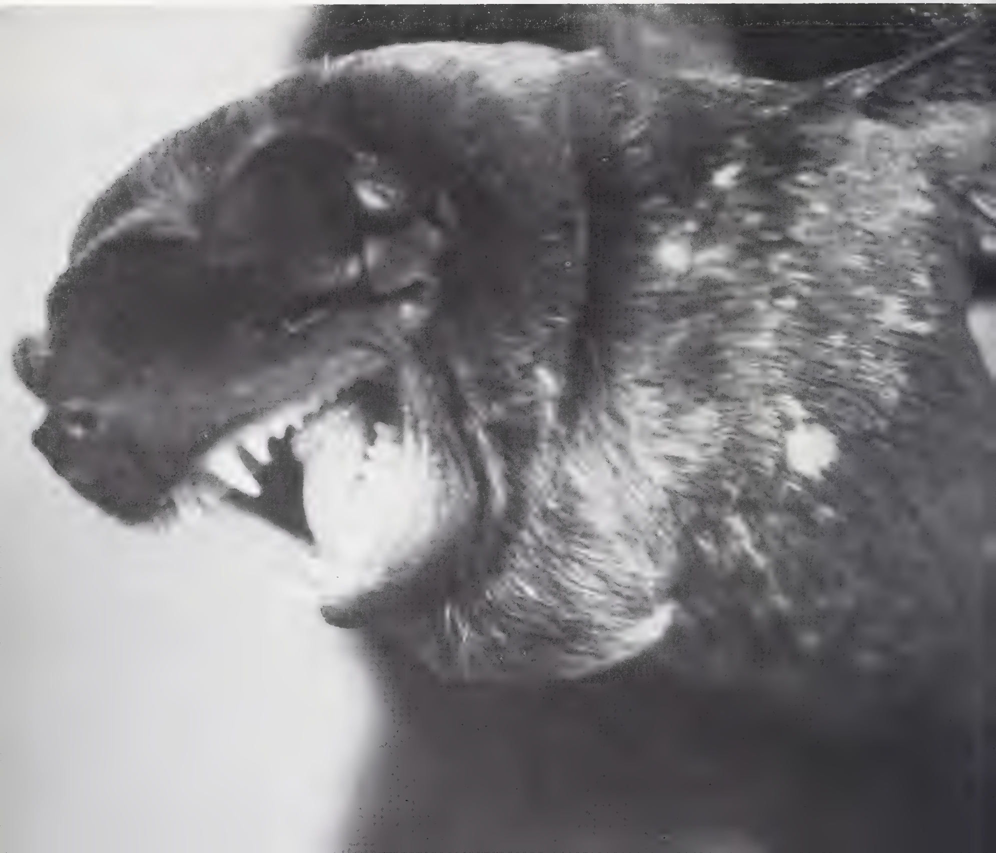
Allen's mastiff bats are found from Sinaloa to Suriname (Fig. 75). Hall (1981) recognized two subspecies as occurring in Costa Rica, *Molossus sinaloae sinaloae* in the north (including La Selva) and *M. s. trinitatus* in the south. Dolan (1982), however, regarded *M. sinaloae* as a monotypic species.

This mastiff bat has been taken in a wide variety of habitats in both wet and dry forest regions, and it commonly roosts in buildings. It is completely insectivorous. The reproductive cycle appears to be continuous (LaVal and Fitch 1977).

Goodwin (1946) reported specimens from Alajuela Province. LaVal and Fitch (1977) reported capturing 76 from a single colony roosting in a building in Puerto Viejo.

Specimens examined (23)—Puerto Viejo, Río Sarapiquí, 70 m [1 male, 7 females, KU; 4 males, 11 females, UMMZ].

Fig. 75. Allen's mastiff bat, *Molossus sinaloae. Photo by R. K. LaVal.*



Tadarida brasiliensis
Brazilian Free-tailed Bat

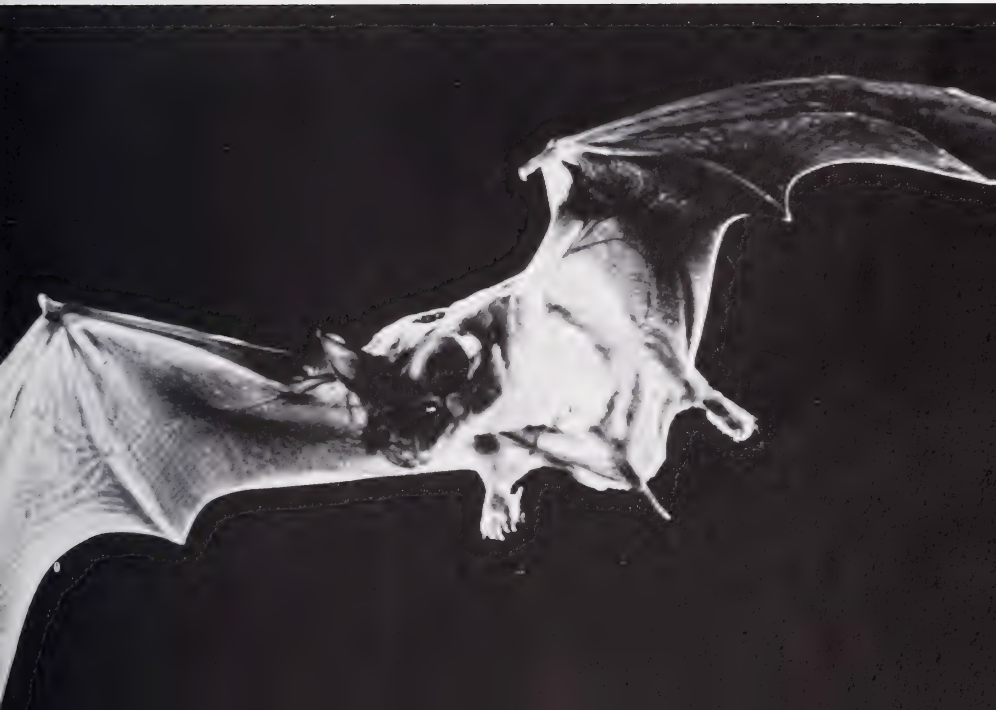
Brazilian free-tailed bats occur from the southern United States to Argentina (Fig. 76). The nominate subspecies, *Tadarida brasiliensis brasiliensis*, occurs throughout Costa Rica and south into South America.

This species is migratory, at least in the northern parts of its range. In Costa Rica, most records have come from higher elevations. Roosts are known from caves, tunnels, bridges, and buildings. The diet is composed entirely of insects. In the northern part of the range, this bat is monestrous and females form huge maternity colonies in summer. The reproductive cycle has not been studied in tropical areas.

Brazilian free-tailed bats were first recorded from Costa Rica by Allen (1892). Starrett and de la Torre (1964) collected 12 from a colony in a building in San José de la Montaña. The male from San Miguel de la Montaña was collected from a colony of perhaps a couple of hundred individuals that roosted in the hollow walls of a home. The volume of urine produced by this colony was so great that the walls were badly stained and the house smelled strongly of urine.

Specimens examined (13)—San José de la Montaña, 1,520 m [1 male, 11 females, LACM]; San Miguel de la Montaña, el. 1,690–1,700 m [1 male, KU]; Vara Blanca [LSUMZ].

Fig. 76. Brazilian free-tailed bat, *Tadarida brasiliensis*. *Photo by M. D. Tuttle.*



ORDER PRIMATES

Primates currently are protected throughout Costa Rica, and probably little poaching occurs. However, historically in this region, spider, howler, and capuchin monkeys were a meat source. Use of these primates for food continued in some areas of Costa Rica as late as the early 1970's, and undoubtedly the indigenous Indians in remote areas are still harvesting them. As the monkeys at La Selva in recent years have received complete protection from hunters, they are undoubtedly less wary of humans. Perhaps their recent abundance is attributable to a decrease in wariness and thus increased visibility as well as an increase in absolute numbers.

Primate populations throughout much of the Caribbean lowlands of Central America were decimated by an epidemic of mosquito-borne yellow fever during the early 1950's (see Fishkind and Sussman 1987, and references therein). Although data are not available for La Selva or the adjacent Braulio Carrillo region, we assume that this epidemic had a tremendous negative effect on the populations of indigenous primates. Far fewer primates were observed at La Selva during the late 1960's, 1970's, and early 1980's than in similar tracts of primary forest elsewhere in the Neotropics. During the past several years, however, primate populations at La Selva have certainly rebounded. It is now common to see capuchin, howler, and spider monkeys almost daily and often in large troops.

Family Cebidae

Alouatta palliata

Mantled Howler Monkey, Mono Congo or Mono Aullador

Mantled howler monkeys are found from southern Mexico south through Central America to extreme northwestern South America, where they occur on the western slope of the Andes in Colombia and Ecuador to Guayaquil (Fig. 77). Two subspecies are found from sea level to forested high elevations (2,500 m) in Costa Rica. The nominate race, *Alouatta palliata palliata*, is widespread in Costa Rica, including Parque Nacional Braulio Carrillo; *A. p. aequatorialis* is restricted to extreme southwestern Costa Rica on the Osa Peninsula. This species adapts well to the presence of humans, usually being as abundant near rural towns and in second growth forests as it is in primary forests.

Howler monkeys were seen or heard by us on numerous occasions in the park from the lower elevations to 1,200 m. Although they are widespread in Costa Rica, howler monkeys are less abundant within Parque Nacional Braulio Carrillo than we have observed them to be in other areas of the country. Additionally, both howler monkeys and white-faced capuchins were wary of us, suggesting that they have been hunted in this area. Corroborating this is Vaughan's (1972) observation of howler monkeys that were shot for human consumption in the vicinity of Cariblanco.

Howler monkeys were observed along the trail from 100 to 200 m; calling troops heard at 200, 300, and 700 m; and a troop observed at 500 m. This is a commonly reported species at La Selva, although it is not as abundant there as are white-faced capuchins (Timm, in press). These monkeys have been seen or heard howling at La Selva in every month of the year. Troop sizes are variable

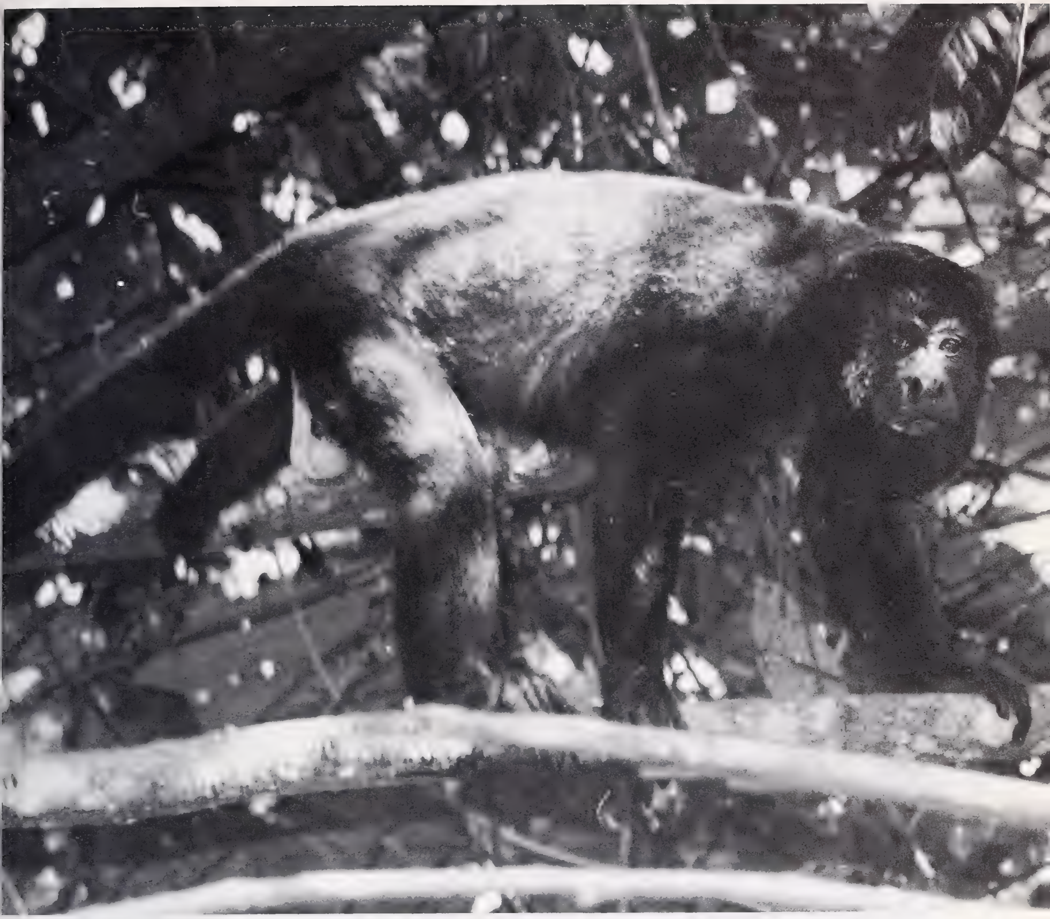


Fig. 77. Mantled howler monkey, *Alouatta palliata. Photo by C. Thorington.*

and may be as high as 10 or 11. Lone individuals, which are usually males, are seen occasionally. Troops that included juveniles were seen in February 1983 (eight adults—three males, five females; two juveniles; and one infant), in April 1983 (three adults—one male, two females; one subadult female; one juvenile; and one infant in natal yellow coat), and in May 1986 (three adults—two males, one female; and one juvenile). Howler monkeys were observed eating the flower buds of *Castilla elastica* in April 1982 and the leaves of *Cecropia* sp. in November 1982; both plants are in the family Moraceae. In the late 1960's only one troop of howler monkeys was known to occur on the La Selva property, but by 1980 two troops were regularly heard. The late foreman of La Selva, Rafael Chavarría, commented that before the 1953 yellow fever epidemic, howlers were extremely abundant along the Río Puerto Viejo.

The biology of howler monkeys in Costa Rica was reviewed by Glander (1980, 1983).

Ateles geoffroyi
Geoffroy's Spider Monkey, Mono Colorado or Mono Araña

Geoffroy's spider monkey is primarily a Central American species found from southern Mexico through Central America to extreme northwestern Colombia (Fig. 78). In Costa Rica, three subspecies currently are recognized, although the group is in need of revision. *Ateles geoffroyi ornatus* is the most widely distributed subspecies in the country and is found in the eastern lowlands and central highlands; *A. g. frontatus* is restricted to the Guanacaste area of Costa Rica and most of Nicaragua; and *A. g. panamensis* is found in southwestern Costa Rica and much of Panama. Spider monkeys are found from sea level to nearly 2,200 m in suitable habitats, which are almost exclusively large tracts of undisturbed primary forest. It is the most widely hunted primate in Costa Rica.

We observed spider monkeys at 200 and 500 m within Parque Nacional Braulio Carrillo and learned that park guards frequently saw them at lower elevations within the park. There are probably at least two *Ateles* troops on the La Selva Biological Reserve, and groups numbering up to 23 individuals have been reported there since mammal records were begun in 1979. It is a commonly reported species at La Selva and has been observed year round. Group sizes vary considerably, but tend to be five or fewer. Lone animals are seen on occasion, and often these are males. Adults with young have been observed from nearly every month of the year; one or two infants may be seen in a troop. On one occasion, an adult male was seen traveling with a troop of six *Cebus*, and on another occasion an adult of unknown sex was with a troop of five *Alouatta*. A mixed group of two or three *Ateles* and five *Cebus* was seen in March 1986. Spider monkeys were observed feeding on the fruits of *Dipteryx panamensis* (Fabaceae) on 25 March 1986, seeds of *Dussia* (Fabaceae) in August and July, fruits of *Protium* (Burseraceae) in February, and fruits of *Dendropanax* (Araliaceae) in September. Rafael Chavarría informed Hartshorn (in litt.) that the large troops of spider monkeys (15 to 30 individuals) broke up during the day into smaller groups (2 to 5 individuals) for foraging. Spider monkeys were rarely observed at La Selva during the early 1970's.

Alston (1879–82:9) reported that spider monkeys were abundant in Costa Rica, "being found in the mountains up to an elevation of from six to seven thousand feet, as well as in the hot forests near the coast." The biology of spider monkeys was reviewed recently by Eisenberg (1983).

Cebus capucinus
White-faced Monkey or White-faced Capuchin, Mono Cara Blanca

White-faced capuchins are found from eastern Honduras and Nicaragua south through Costa Rica to northwestern Colombia and Venezuela (Fig. 79). A single subspecies, *Cebus capucinus imitator*, is found in Costa Rica from sea level to 3,000 m. This species is adapted to a variety of habitat types and, although it is legally protected in Costa Rica, as are the other species of monkeys, it is not endangered. The biology of white-faced monkeys in Costa Rica recently was reviewed by Freese (1983). We have the general impression that all three species of primates

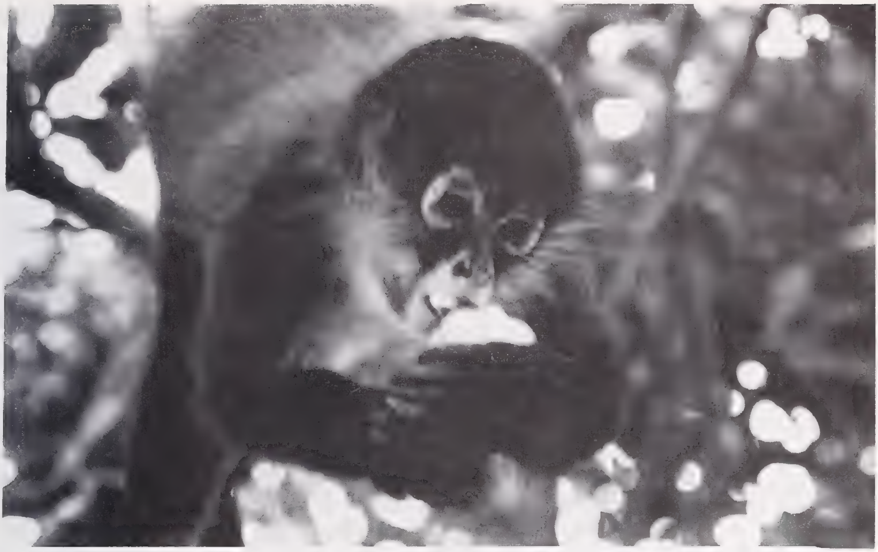


Fig. 78. Geoffroy's spider monkey, *Ateles geoffroyi. Photo by D. E. Wilson.*

are more common at La Selva now than when the Organization for Tropical Studies acquired the property in 1968.

White-faced monkeys are one of the most abundant and frequently seen mammals at La Selva. Individuals can be observed on a daily basis if an effort is made to locate them. There are records from the La Selva property for every month of the year. *Cebus capucinus* is most often seen in groups of four to five; however,

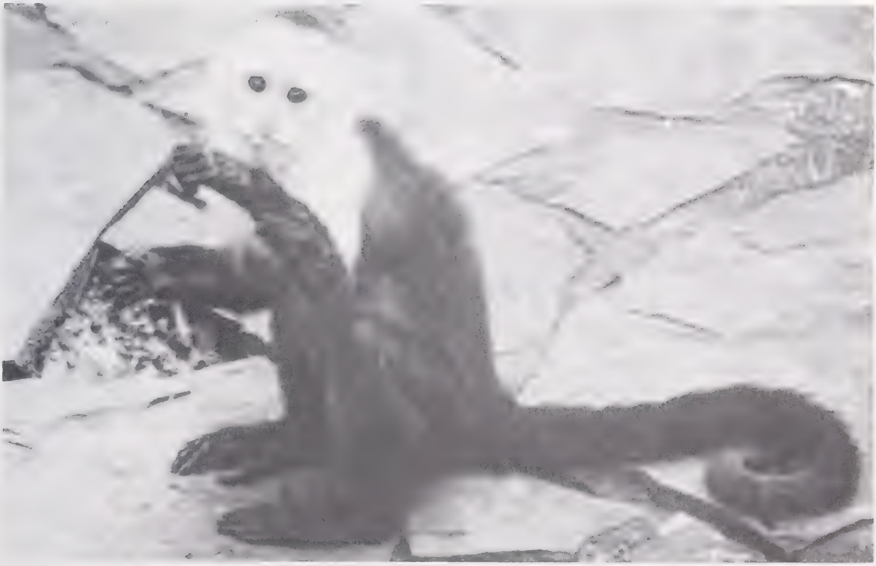


Fig. 79. White-faced capuchin, *Cebus capucinus. Photo by N. Woodman.*

lone individuals, most likely males, have been observed on several occasions. The largest groups observed contained 15 to 20 individuals. Juveniles are first seen in January. On 7 January 1987, seven adults and one juvenile were observed; on 21 January 1987, seven or eight adults and two juveniles were observed; on 22 January 1987, an adult female near term was seen. In May and June of 1986, one or more troops ranging from five to nine adults with two infants were observed on several occasions. On two occasions, troops of *C. capucinus* have been observed in trees adjacent to troops of howler monkeys; on one occasion, a male spider monkey was seen with a troop of capuchins and on another a mixed group of *C. capucinus* and *Ateles geoffroyi* was seen together. On 16 September 1982, five *C. capucinus* were observed eating the fruits of *Pourouma aspera* (Moraceae). They were seen eating *Inga* sp. (Mimosaceae) on 21 October 1982 and fruits of *Minquartia guianensis* (Olacaceae) on 24 October 1982. White-faced monkeys were seen eating the fruits of *Dipteryx panamensis* on 31 July 1983 and those of *Welfia georgii* in April, July, August, and October. They feed by ''breaking off entire rachillae, chewing the exocarp off individual fruits, eating the mesocarp, and dropping the undamaged seeds and the broken rachillae to the ground'' (Vandermeer et al. 1979:19). They are probably important dispersers of *Welfia* seeds.

We observed *Cebus capucinus* on 14 occasions within Parque Nacional Braulio Carrillo at elevations of 100, 300, 700, and 1,540 m. Group sizes of 10 or more were seen between 100 m and 300 m, whereas group sizes were smaller at higher elevations. White-faced capuchins at lower elevations were quiet when approached and frequently retreated quickly and quietly, whereas at higher elevations they often would display aggressive behavior. We interpret this to indicate greater hunting pressures on these monkeys at lower elevations.

ORDER XENARTHRA

Family Bradypodidae

Bradypus variegatus
Three-toed Sloth, Perezoso de Tres Dedos

Three-toed sloths are found from extreme eastern Honduras southward through much of tropical South America (Fig. 80). Two subspecies of three-toed sloths are found in Costa Rica, *Bradypus variegatus castaneiceps* in the north and east, the race at La Selva, and *B. v. griseus* in the west. In Costa Rica, they are abundant in moist forests from sea level to elevations of 500 to 600 m. *Bradypus variegatus* is officially protected in Costa Rica as an endangered species, although we suspect that these animals are found in good numbers in appropriate habitats as indicated by Montgomery and Sunquist from their studies of three-toed sloths on Barro Colorado Island, Panama. Their apparent rarity probably stems from the fact that they are often difficult to see.

Three-toed sloths have been sighted on many occasions at La Selva. Interestingly, most of these records are from the dry season (December through April). This

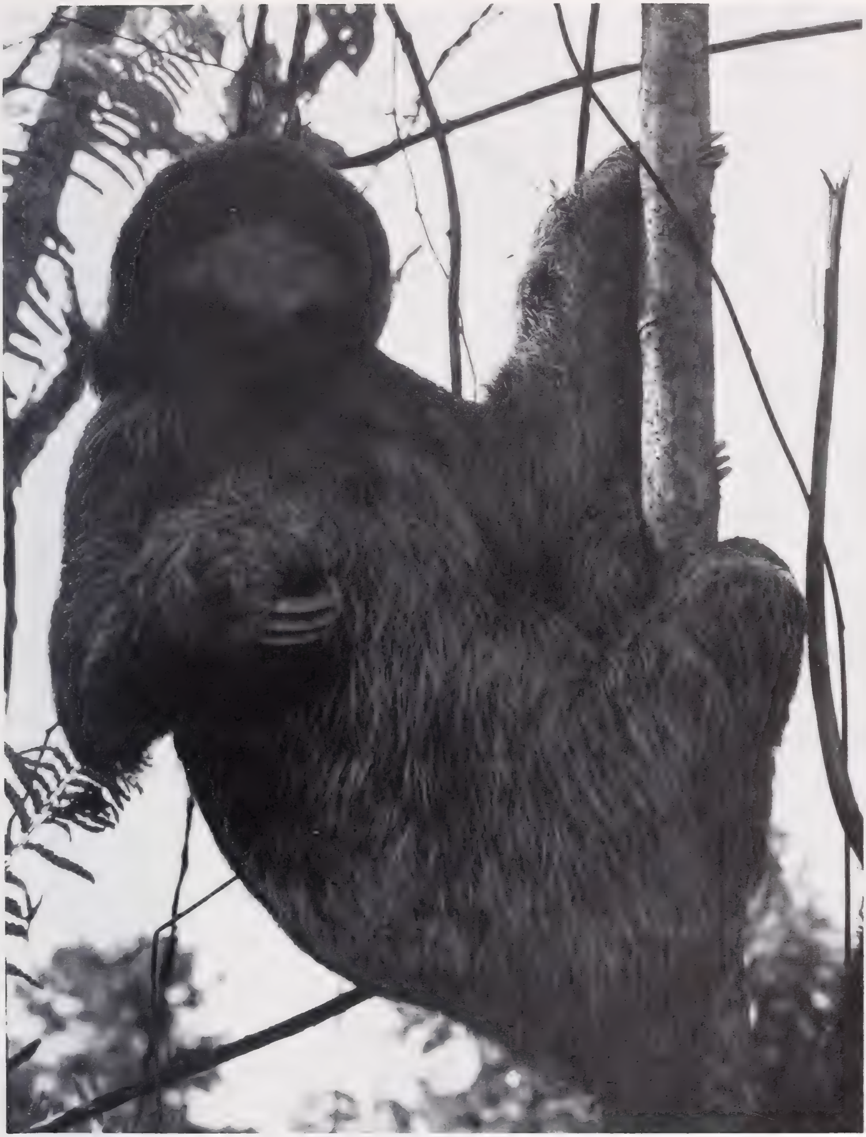


Fig. 80. Three-toed sloth, *Bradypus variegatus. Photo by R. M. Timm.*

probably indicates that they are more visible during these months either because they are moving more or they are just more easily seen in their preferred trees. Several of the observed animals were in *Cecropia* trees, one of the favored food sources of this species. They are often visible from the foot bridge over the Río Puerto Viejo, where they can be seen in the *Cecropia* trees on the south bank. We observed a single three-toed sloth in Parque Nacional Braulio Carrillo at 200 m in March 1986.

Greene (in press) observed an aggressive interaction between two adult male three-toed sloths at La Selva. This is the first such observation on free-ranging sloths. He saw one sloth actively approach the other in a *C. obtusifolia* tree and witnessed that they struck each with their forefeet and emitted high pitched vocalizations. The aggressive encounter lasted some 3 min and ended when one sloth rapidly descended the tree. He also reported that 4 days later on 19 December 1987 ''a pregnant female sloth was seen in the same tree, and one week later a female with young was seen ca. 100 m away.'' Greene (in press) concluded that these observations suggest that the social system and other natural history traits of sloths were more complex than has been previously thought. Sloths are one of the primary prey items taken by jaguars at La Selva (Greene, in litt.).

A discussion of the taxonomy of algae found in sloth hair was provided by Wujek and Timpano (1986) who described a blue-green alga, a branched, filamentous red alga, and two species of coccoid green algae based in part on material collected on sloths at La Selva.

The biology of three-toed sloths, primarily summarized from research on Barro Colorado Island, Panama, was reviewed recently by Montgomery (1983a). Excellent comprehensive reviews on the biology of sloths and other xenarthrans were provided by Montgomery (1978, 1985).

Specimens examined (2)—Puerto Viejo, Río Sarapiquí, 300 ft [2 females, UMMZ].

Family Choloepidae

Choloepus hoffmanni
Two-toed Sloth, Perezoso

Two-toed sloths are found from southeastern Nicaragua to northwestern Venezuela and Colombia (Fig. 81). The subspecies *Choloepus hoffmanni hoffmanni* is found throughout Costa Rica from sea level to at least 1,800 m.

Two-toed sloths have been sighted on 14 occasions at La Selva. Observations of this species have been made throughout the year. Adults accompanied by single young have been seen on three occasions—twice during January and once in March. We observed a single two-toed sloth at 200 m in Parque Nacional Braulio Carrillo in March 1986.

Specimens examined (2)—Volcán Barva [1 female, CAL; 1 female, MVZ].

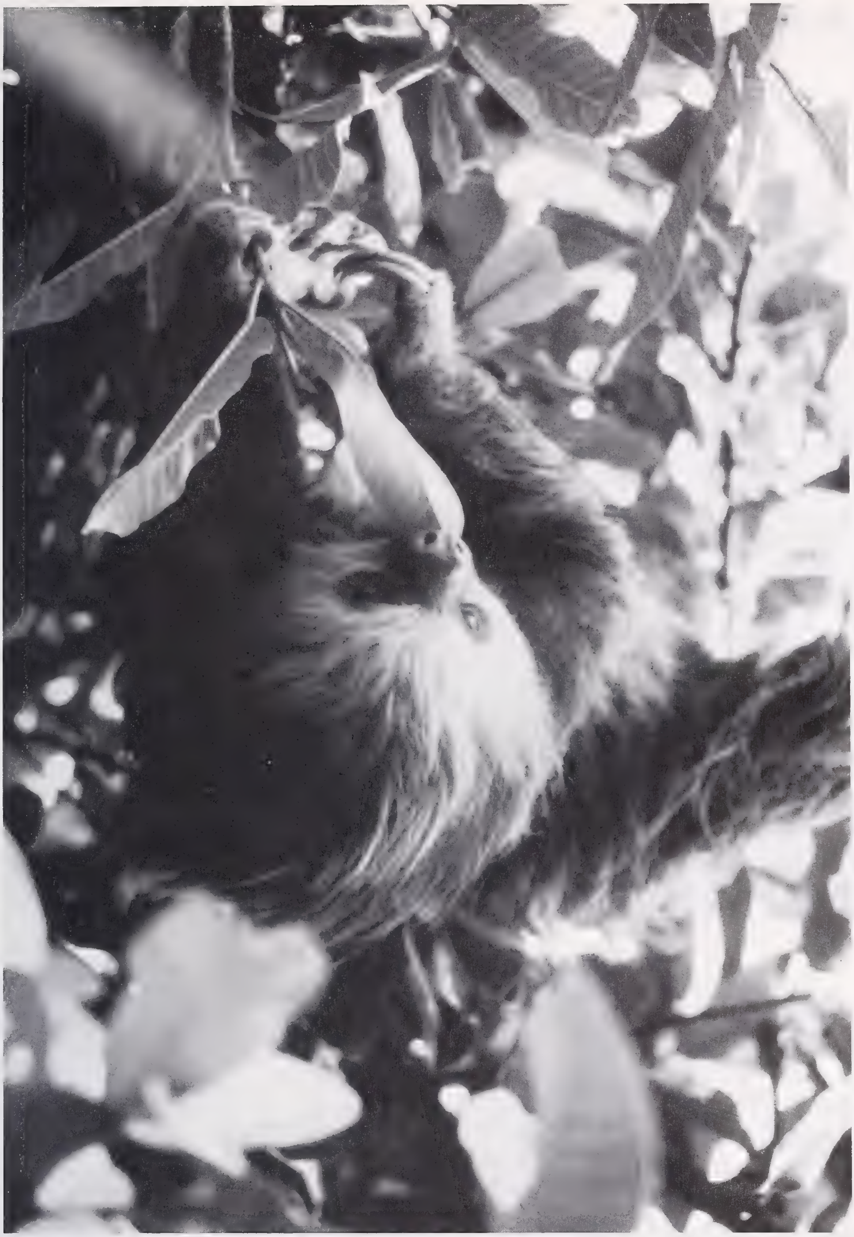


Fig. 81. Two-toed sloth, *Choloepus hoffmanni. Photo by B. L. Clauson.*

Family Dasypodidae

Cabassous centralis
Central American Five-toed Armadillo, Armadillo Zopilote

Central American five-toed armadillos are found from southeastern Guatemala to northwestern Venezuela (Fig. 82). In Costa Rica, they are found from sea level to 1,800 m. *Cabassous centralis* is a monotypic species (Wetzel 1980).

In March 1986 we observed Central American five-toed armadillos in Parque Nacional Braulio Carrillo at about 200 m. *Cabassous centralis* has been observed at La Selva on only three occasions: 1973, August 1983, and December 1984.

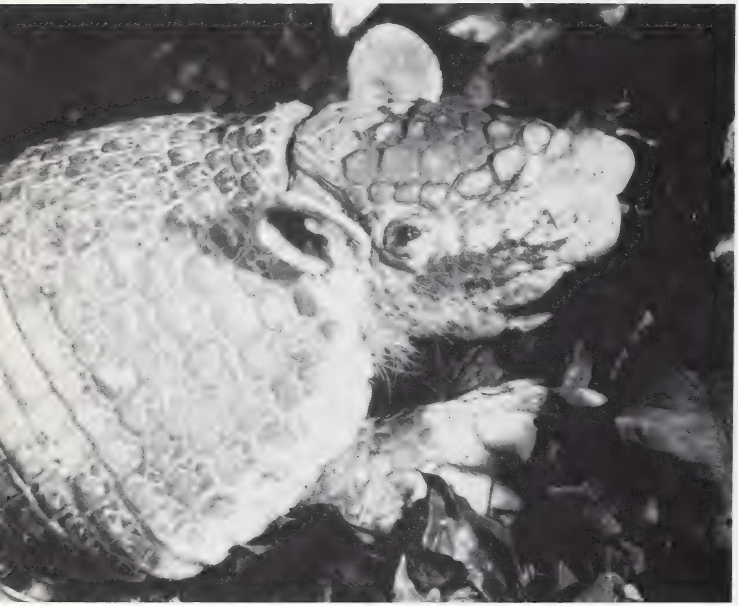


Fig. 82. Central American five-toed armadillo, *Cabassous centralis. Photo by R. K. LaVal.*

Dasypus novemcinctus
Nine-banded Armadillo, Cusuco

Nine-banded armadillos are the most widely distributed xenarthrans, occurring from the southeastern United States to southeastern Brazil and northeastern Argentina (Wetzel 1982; Fig. 83). The subspecies *Dasypus novemcinctus fenestratus* is found throughout Costa Rica, except at higher elevations.

Armadillos have been noted at La Selva on many occasions. They have become so abundant in recent years that they can be seen nearly every evening. An adult female and her litter of four half-grown young were sighted by us on several occasions in August 1988. One armadillo was observed by us in March 1986 at 200 m. Pringle et al. (1984) reported sighting an armadillo along the trail east of the Quebrada Cantarrana base camp in January 1983.

The biology and distribution of *Dasypus novemcinctus* recently was reviewed by McBee and Baker (1982) and Wetzel (1983, 1985).

Specimen examined (1)—4 mi N of Barva, Hwy. 9 [1 male, LACM].

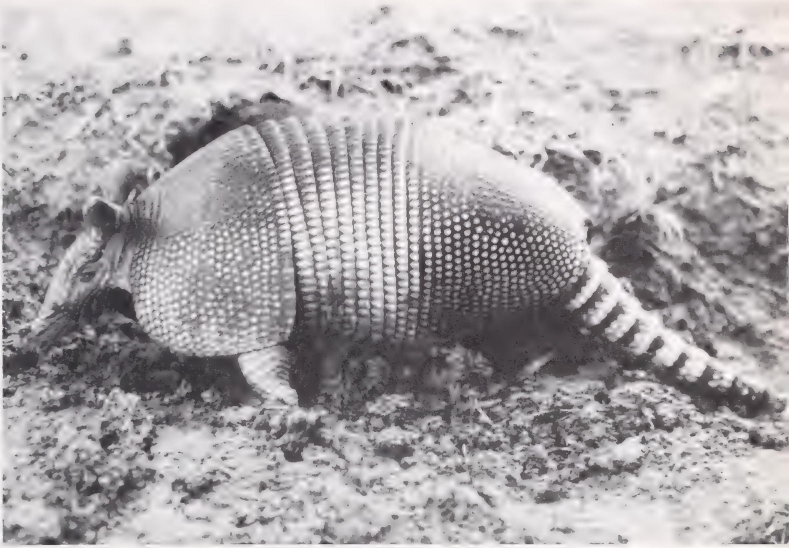


Fig. 83. Nine-banded armadillo, *Dasypus novemcinctus. Photo by B. L. Clauson.*

Family Myrmecophagidae

Cyclopes didactylus

Silky Anteater, Serafín de Platanar or Tapacara

Silky anteaters are known from southern Mexico to northern South America (Fig. 84). The subspecies *Cyclopes didactylus dorsalis* is found throughout the tropical humid zone of Costa Rica up to about 1,500 m.

Silky anteaters have been observed on 11 occasions at La Selva. As with the sloths, we believe that they are present in the lower elevations of Parque Nacional Braulio Carrillo. However, there are no records from Braulio Carrillo, probably because they are difficult to observe. The biology of silky anteaters recently was reviewed by Montgomery (1983b).

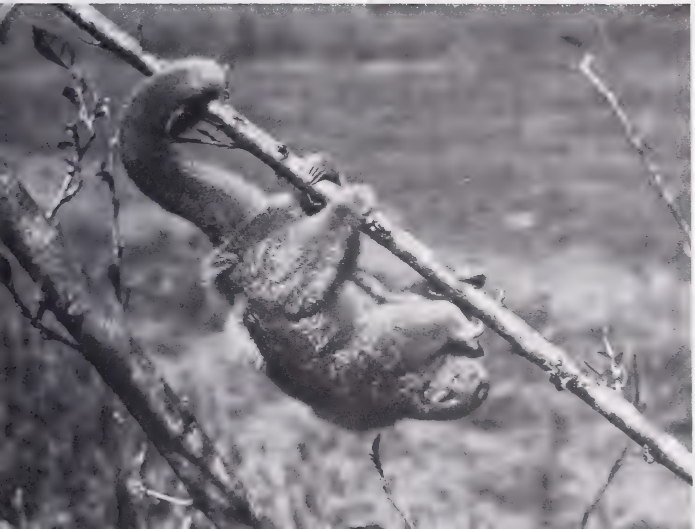


Fig. 84. Silky anteater, *Cyclopes didactylus. Photo by R. W. McDiarmid.*

Tamandua mexicana
Northern Tamandua, Oso Hormiguero

Northern tamanduas are found from southern Mexico to northwestern Venezuela, western Colombia, western Ecuador, and western Peru (Fig. 85). The subspecies *Tamandua mexicana chiriquensis* occurs throughout Costa Rica from sea level to 1,500 m.

Tamanduas commonly are encountered at La Selva where they have been seen as lone individuals year round. Many observations of these animals were during the day when they were active. A lone juvenile tamandua was seen at La Selva on 20 April 1988. An adult female was captured alive on 17 April 1986 (3 km S, 11.5 km E of San Miguel, 1,400 m) and released after being photographed. A second tamandua was spotted during midday on 27 March as it traveled near the 300-m base camp, about 10 km S, 9.5 km W of Puerto Viejo. It appeared to be an adult, but no attempt was made to capture the animal. Pringle et al. (1984) reported a tamandua in January 1983 on the trail east of the Quebrada Cantarrana base camp.

Additionally, an adult female was found dead on Route 9 just northeast of La Virgen, 180 m, on 8 June 1982 by Timm. The biology of tamanduas in Costa Rica was reviewed recently by Lubin (1983).

Specimen examined (1)—La Virgen, 180 m [1 female, FMNH].

ORDER LAGOMORPHA

Family Leporidae

Sylvilagus brasiliensis
Forest Rabbit or Forest Cottontail, Conejo

Forest rabbits occur from the eastern and southern lowlands of Mexico through Central America and South America to northern Argentina and southern Brazil (Fig. 86). In Costa Rica the subspecies *Sylvilagus brasiliensis gabbi* is found in the Caribbean lowlands (Diersing 1981).

Forest rabbits have been recorded in the log book at La Selva on only 13 occasions in the early 1980's; however, they are now seen frequently in the station clearing and along the Sura trail. Also, it was not uncommon to see forest rabbits in the clearings around the laboratory buildings in 1977 and 1978. Forest rabbits are more common in the successional plots and in clearings at La Selva than in primary forest. Hoth (in litt.) observed at night a single pair for a period of 2 weeks in August 1987. During that time he saw several copulations. A 2-m long fer-de-lance (*Bothrops asper*) captured on 5 July 1978, in disturbed habitat at La Selva, contained an adult *S. brasiliensis* (Findley, in litt.). In January 1983, forest rabbits occasionally were seen in grass along the trail east of the Cantarrana base camp (Pringle et al. 1984).

Specimens examined (7)—Puerto Viejo, Río Sarapiquí, 300 ft [5 males, 1 female, UMMZ]; 1.7 mi S of Puerto Viejo [1 male, LACM].

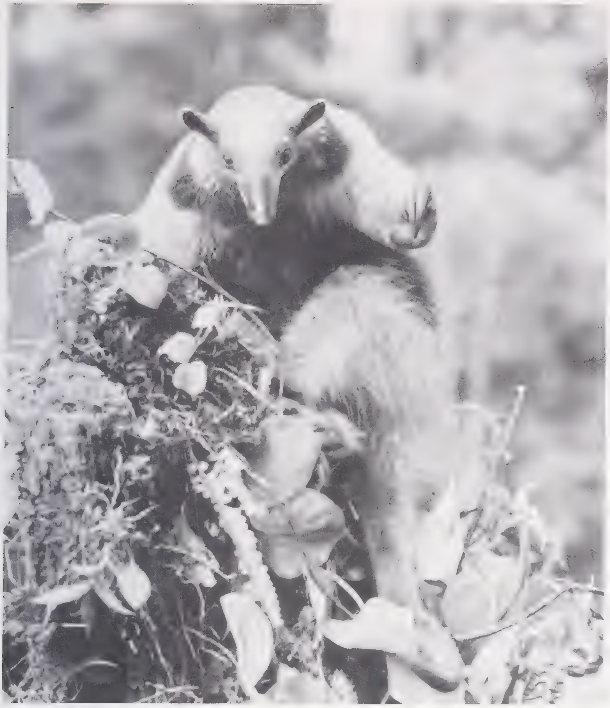
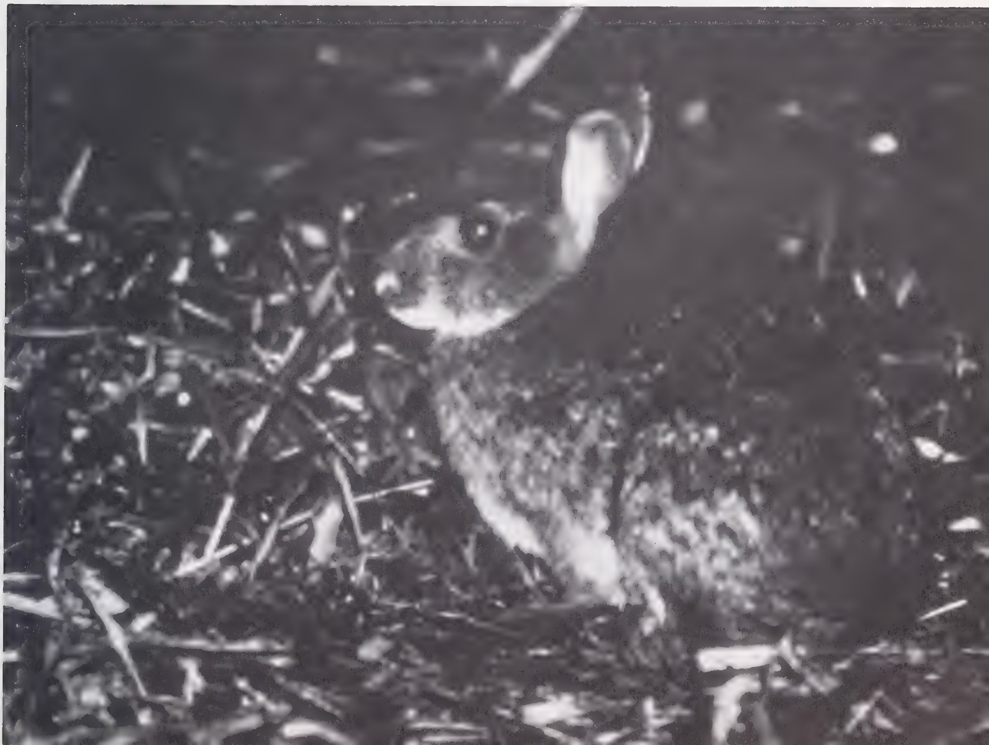


Fig. 85. Northern tamandua, *Tamandua mexicana. Photo by B. L. Clauson.*

Fig. 86. Forest rabbit, *Sylvilagus brasiliensis. Photo by J. Hoth.*



Sylvilagus dicei
Dice's Cottontail, Conejo

Dice's cottontail is restricted to elevations above 1,100 m in the Cordillera de Talamanca of Costa Rica and adjacent west-central Panama. There are no recognized subspecies of *Sylvilagus dicei*. *Sylvilagus dicei* originally was described by Harris (1932) based on specimens from El Copey de Dota in the Cordillera de Talamanca. Most subsequent authors have followed Hershkovitz (1950) in regarding *dicei* as a subspecies of *S. brasiliensis*; however, Diersing (1981) recently demonstrated that this is a separate species of cottontail rabbit.

We observed at night a single cottontail rabbit on a trail near the 2,600-m base camp. Although there are no specimens of cottontail rabbits from Parque Nacional Braulio Carrillo, based on their known distribution and systematics, rabbits at lower elevations are probably *S. brasiliensis* and those at higher elevations probably are *S. dicei*. Dice's cottontails are an important component of the diet of coyotes (*Canis latrans*) in the Costa Rican highlands (Vaughan and Rodriguez 1986).

ORDER RODENTIA

Family Sciuridae

Microsciurus alfari
Alfaro's Pygmy Squirrel, Ardilla or Chiza

Alfaro's pygmy squirrels are found from southern Nicaragua to northwestern Colombia. Three subspecies are known from lower and middle elevations of northeastern Costa Rica: *Microsciurus alfari alfari* (the subspecies occurring at La Selva), *M. a. alticola*, and *M. a. septentrionalis*. A fourth subspecies, *M. a. browni*, is found in the southwestern lowlands.

Pygmy squirrels have been noted at La Selva on 12 occasions; on 4 observations, 2 squirrels were seen together and the remaining 8 observations were of lone individuals. In February 1985, a pygmy squirrel was seen feeding on the fruit of *Dipteryx panamensis*, a common canopy tree at La Selva. A semiplumbeous hawk (*Leucopternis semiplumbea*) was seen diving at, but missing, a pygmy squirrel in April 1982. In January 1987, we watched 2 individuals as they spent 10 min moving about on lianas attached to a huge *Ceiba pentandra*. They descended and crossed the ground to an adjacent tree. Pygmy squirrels were observed by the 1983 Zona Expedition (Pringle et al. 1984).

Specimens examined (2)—Río Sarapiquí, Puerto Viejo, 300 ft [1 male, UMMZ]; La Hondura, Province San José [1, UMMZ; Harris 1943].

Sciurus granatensis
Tropical Red-tailed Squirrel, Ardilla or Chiza

Tropical red-tailed squirrels range from Costa Rica south to Ecuador and Venezuela (Fig. 87). Two subspecies are now recognized from Costa Rica: *Sciurus granatensis hoffmanni* in the central highlands and *S. g. chiriquensis* in the

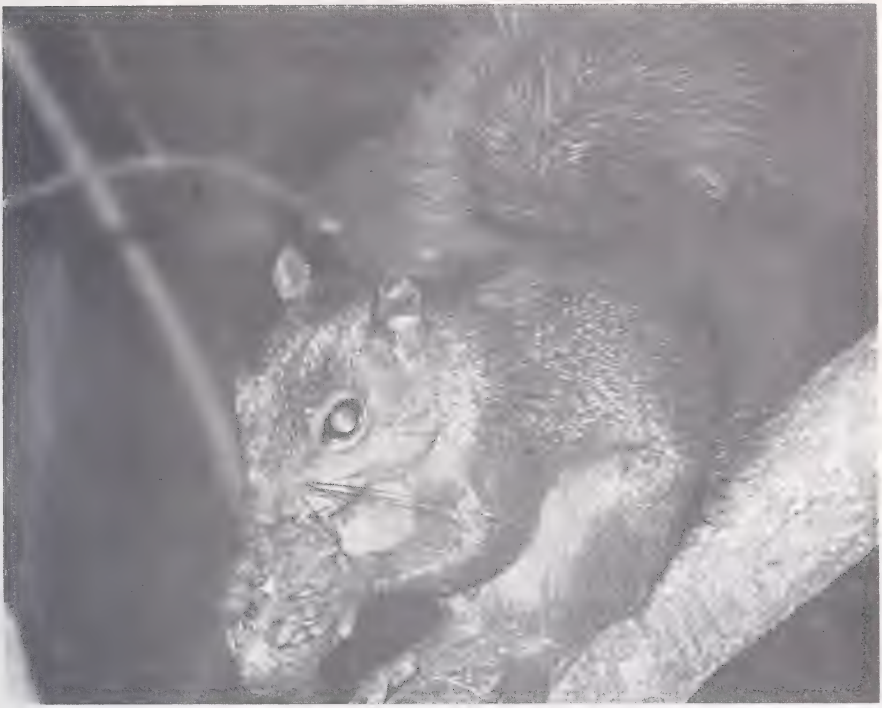


Fig. 87. Tropical red-tailed squirrel, *Sciurus granatensis. Photo by C. Thorington.*

surrounding lower elevations including the La Selva area. These squirrels occur from sea level to about 1,500 m.

Sciurus granatensis was seen on several occasions within Parque Nacional Braulio Carrillo at elevations ranging from 100 to 860 m. In the forest near the 300-m base camp, one individual was observed on several days in succession. We have observed red-tailed squirrels on several occasions at La Selva. In the mammal logbook at La Selva there are several records listed of medium-sized *Sciurus* identified as *S. deppei*. We suspect that most, if not all, of these observations are actually *S. granatensis*.

In Panama, *S. granatensis* eats a wide variety of plants, but the large, nutlike fruits of three species, *Astrocaryum standleyanum*, *Dipteryx panamensis*, and *Scheelea zonensis*, make up most of the diet. The reproductive season of tropical red-tailed squirrels is strongly correlated to the seasonal availability of these three preferred fruits. Adult females were found to have an average of two litters per year and a mean of 1.9 young per litter (Glanz et al. 1982). The biology of these squirrels was reviewed recently by Heaney (1983) and Nitikman (1985).

Specimens examined (3)—Puerto Viejo, Río Sarapiquí, 300 ft [1 female, UMMZ]; San José de la Montaña [2, UNA].

Additional record (1)—2 mi SE of Cariblanco [1 male, MVZ].

Sciurus variegatoides
Variegated Squirrel, Ardilla or Chiza

Variegated squirrels are found from southern Mexico to Panama (Fig. 88). In Costa Rica, as many as eight subspecies of *Sciurus variegatoides* have been reported (Hall 1981); however, the color patterns of this squirrel are quite variable geographically and its subspecific taxonomy is in need of revision. The subspecies of variegated squirrel thought to be represented in northeastern Costa Rica is *Sciurus variegatoides thomasi*. Variegated squirrels are often abundant at low and middle elevations. We have found them as high as 1,850 m.

Variegated squirrels have been recorded on only 10 occasions in the mammal logbook at La Selva. We saw one near the El Sura bridge in January 1987.

Specimens examined (2)—Barva, San Miguel de la Montaña, 1,800 m [1 male, KU; 1 male, UNA].

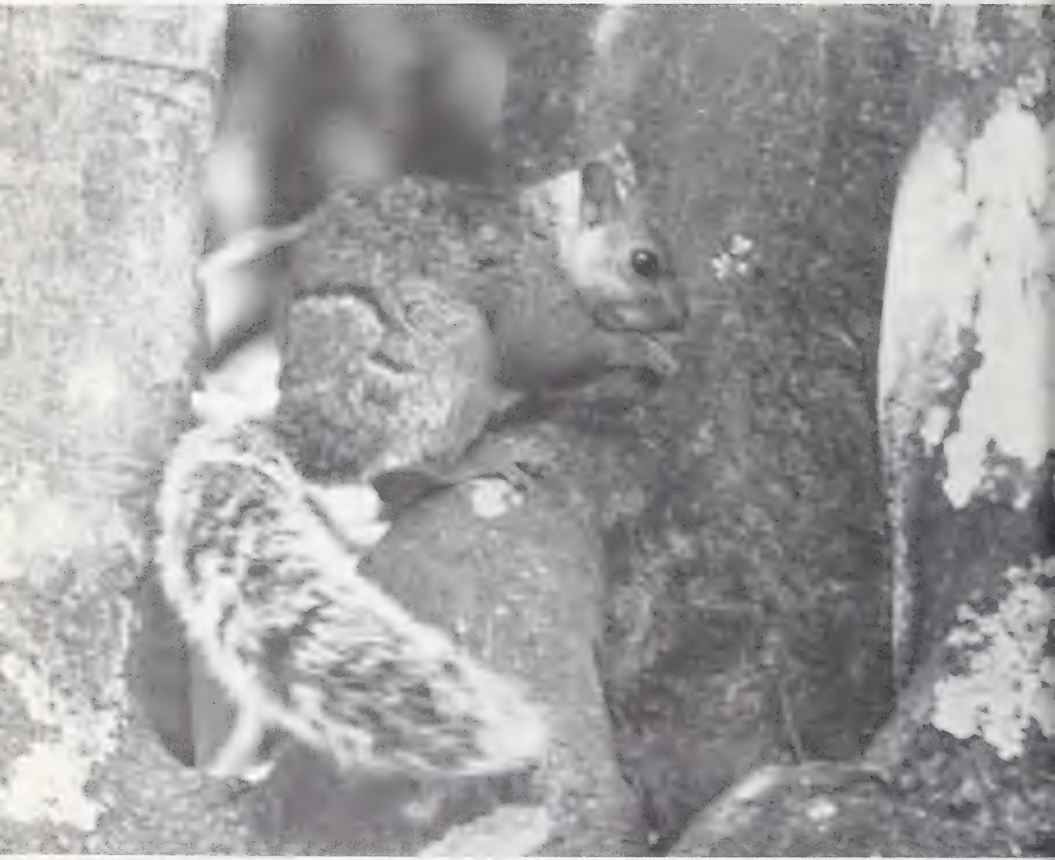


Fig. 88. Variegated squirrel, *Sciurus variegatoides. Photo by R. M. Timm.*

Family Geomyidae

Orthogeomys cherriei

Cherrie's Pocket Gopher, Taltusa

Cherrie's pocket gopher, *Orthogeomys cherriei*, previously was thought to be restricted to low elevations of central and northern Costa Rica; however, it has been documented recently that this species occurs in a broad elevational band (from 50 to 1,450 m) north and east of the Cordillera Central and north and west of the Cordillera de Tilaran in northern Costa Rica (Hafner and Hafner 1987; Fig. 89). Although there are no specimens of pocket gophers from La Selva or Parque Nacional Braulio Carrillo, we know that they occur in these regions and we suspect that the species is *O. cherriei*. *Orthogeomys cherriei* is abundant in the vicinity of Santa Clara, Limón Province, where it does considerable damage to bananas. Pocket gophers are difficult to locate in forests; we suspect that in lowland forests they only occur in the more fertile soils that have little rock and are fairly well drained. Pocket gophers are often more abundant in disturbed habitats than they are in pristine forests.

Pocket gophers destroyed L. R. Holdridge's original plantation of Para rubber trees, *Hevea brasiliensis* (Euphorbiaceae), at La Selva in the late 1950's. Hartshorn (in litt.) has seen the destruction of the basal meristem of young *Welfia georgii* palms by pocket gophers in primary forest at La Selva. Large populations of pocket gophers in the Puerto Viejo region cause severe damage to agricultural crops, especially bananas, platano, and yuca, with some farmers reporting as much as a 50% crop loss (Sisk and Vaughan 1984).

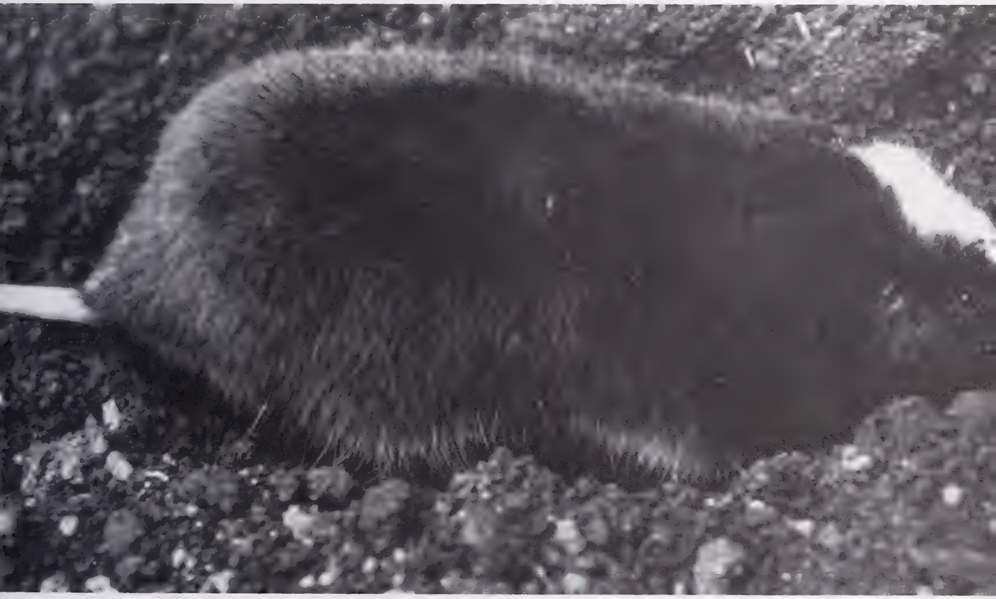


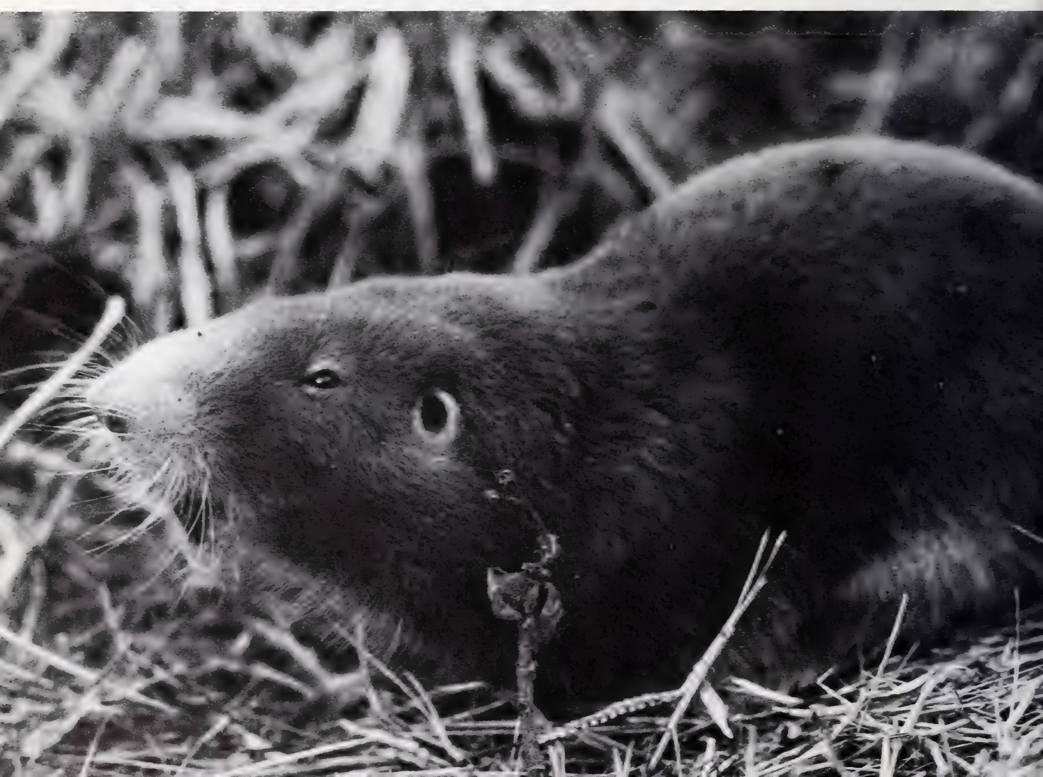
Fig. 89. Cherrie's pocket gopher, *Orthogeomys cherriei. Photo by R. K. LaVal.*

Orthogeomys heterodus
Variable Pocket Gopher, Taltusa

The variable pocket gopher, a species endemic to Costa Rica, is known from the mid- and high elevations of the Cordillera Central and Cordillera de Talamanca (Fig. 90). Three subspecies of *Orthogeomys heterodus* currently are recognized from Costa Rica, but we know little of its systematics, distribution, or ecology. The subspecies *O. h. cartagoensis* occurs on the northeastern Caribbean slope and in the adjacent central valley. Although there are no specimens of *O. heterodus* from Braulio Carrillo, this species is known from just outside the park near Concepción de San Rafael de Heredia and elsewhere in Heredia Province, and we suspect that it occurs in the park also.

In a study of several aspects of the natural history of *O. heterodus* near Concepción, Sisk and Vaughan (1984) found that variable pocket gophers had extensive tunnel systems that consisted of three parts: an enlarged central chamber or nest, radiating tunnels that connect the nest with foraging areas, and a network of shallow feeding tunnels. They found multiple foraging areas within the territory, a foraging strategy previously unreported in pocket gophers. Activity periods consisted of short excursions from the nest area to foraging areas, with 90% of the time spent near the nest. The average home range for two gophers was 237 m^2 (Sisk and Vaughan 1984).

Fig. 90. Variable pocket gopher, *Orthogeomys heterodus. Photo by N. Woodman.*



Family Heteromyidae

Heteromys desmarestianus

Desmarest's Spiny Pocket Mouse, Ratón Semiespinosa

Desmarest's spiny pocket mouse is found from extreme southern Mexico to Colombia (Fig. 91). Five subspecies of *Heteromys desmarestianus* currently are recognized from Costa Rica; the race at La Selva being *H. d. subaffinis*. It is found from sea level to high elevation cloud forest and may be extremely abundant locally (Fleming 1983b).

Heteromys desmarestianus is the most abundant forest floor rodent at La Selva and is found in a wide array of forested habitats (Fleming 1974a,b, 1977a,b). However, it is uncommon or absent in the successional plots at La Selva. All females weighing more than 66 g were pregnant in April 1986 (Table 1). Mean testes length and width for eight adult males was 19.8×13.1 mm. Spiny mice were found carrying seeds of the following plants in their cheek pouches: *Euterpe macrospadix*, *Geonoma* sp., *Iriartea gigantea* (Palmae), and *Meliosma* sp. (Sabiaceae). Bushmasters (*Lachesis muta*) are abundant at La Selva and often are found coiled near *Welfia* palms, the preferred food of spiny mice (Fleming and Brown 1975). It is likely that spiny mice constitute one of the principal food items of bushmasters.

We found one species of sucking louse, *Fahrenholzia ferrisi* (Hoplopleuridae), to be abundant on *H. desmarestianus*. In April 1986, we found all life cycle stages including eggs, first, second, and third instars, and adults, primarily on the dorsal surface of hosts.

Fig. 91. Desmarest's spiny pocket mouse, *Heteromys desmarestianus*. *Photo by B. L. Clauson.*

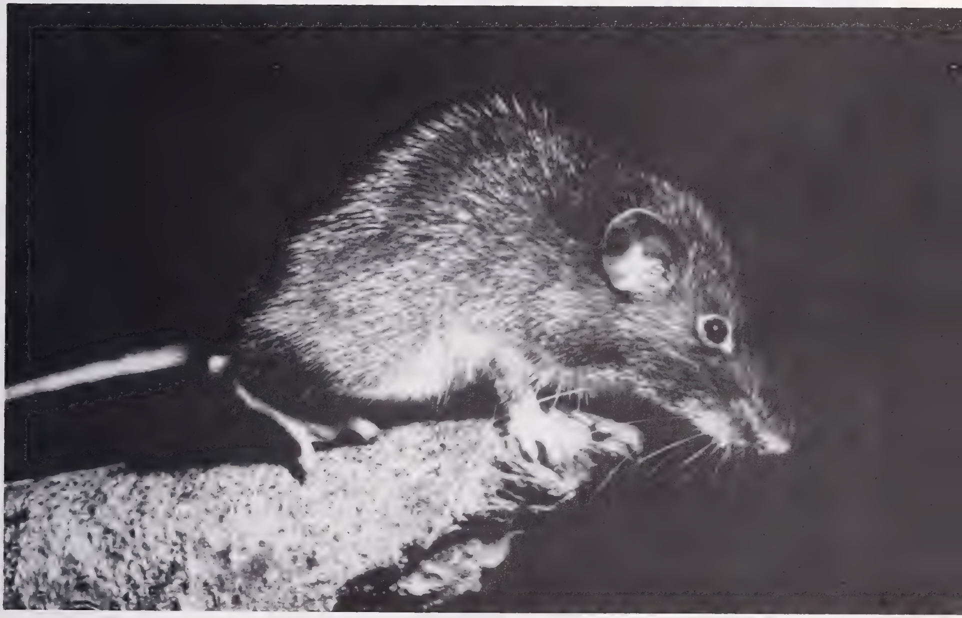


Table 1. *Reproductive characteristics of five adult (weight > 66 g) female* Heteromys desmarestianus *from Heredia Province, Costa Rica.*[a]

Date of capture	Reproductive characteristics
29 March 1986	3 embryos × 12 mm (2L–1R), lactating
30 March 1986	pregnant female, mammae enlarged; released
5 April 1986	2 embryos × 22 mm (1L–1R) plus 1 resorbing embryo
5 April 1986	3 embryos × 23 mm (1L–2R)
8 April 1986	uterus enlarged, no embryos or placental scars

[a] Eight females weighing between 45 and 66 g showed no sign of reproductive activity. All females weighing more than 66 g were reproductively active.

A tineid moth, *Amydria selvae*, phoretic on *H. desmarestianus*, was described by Davis et al. (1986) from La Selva. Only females of *A. selvae* were found on spiny pocket mice; no males were collected. All specimens were taken in July 1984. *Heteromys desmarestianus* was trapped in both lowland and highland localities and at La Selva in late August and September, but no additional moths were found (Davis et al. 1986). We examined 47 *H. desmarestianus* captured from 280 to 1,520 m elevation in late March and April 1986 in Parque Nacional Braulio Carrillo but found no tineids. Nor were any tineids found on 120 *H. desmarestianus* caught near Monteverde, Puntarenas Province at elevations ranging from 1,380 to 1,860 m in May 1986. Ticks found on *H. desmarestianus* included four adult female *Ixodes venezuelensis*. This represents the first record of this tick on *H. desmarestianus*.

Specimens examined (255)—Finca La Selva, 3 km S of Puerto Viejo [1 male, 2 females, KU; 9 males, 5 females, LACM; 101 males, 99 females, UMMZ]; Puerto Viejo, Río Sarapiquí [1 female, KU]; 1.7 mi S of Puerto Viejo [1 male, LACM]; 3.2 mi S of Puerto Viejo [1 female, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 280, 325, 340, 365, and 369 m [2 males, 8 females, FMNH; 1 male, UNA]; 1 km S, 11.5 km E of San Miguel, 680, 700, 710 m [6 males, 8 females, FMNH; 1 male, 1 female, UNA]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [3 males, 2 females, FMNH]; 9 km S, 11.5 km E of San Miguel, 1,520 m [1 male, 2 females, FMNH].

Family Muridae

Nyctomys sumichrasti
Sumichrast's Vesper Rat, Ratón

Sumichrast's vesper rat is found from Mexico to eastern Panama (Fig. 92). Three subspecies of *Nyctomys sumichrasti* occur in Costa Rica, *N. s. costaricensis* along the Pacific slopes, *N. s. nitellinus* in the southeast, and *N. s. venustulus* in the northeast. It is found from sea level to 1,500 m. Ecology and morphological variation in vesper rats in Nicaragua were reported by Genoways and Jones (1972).

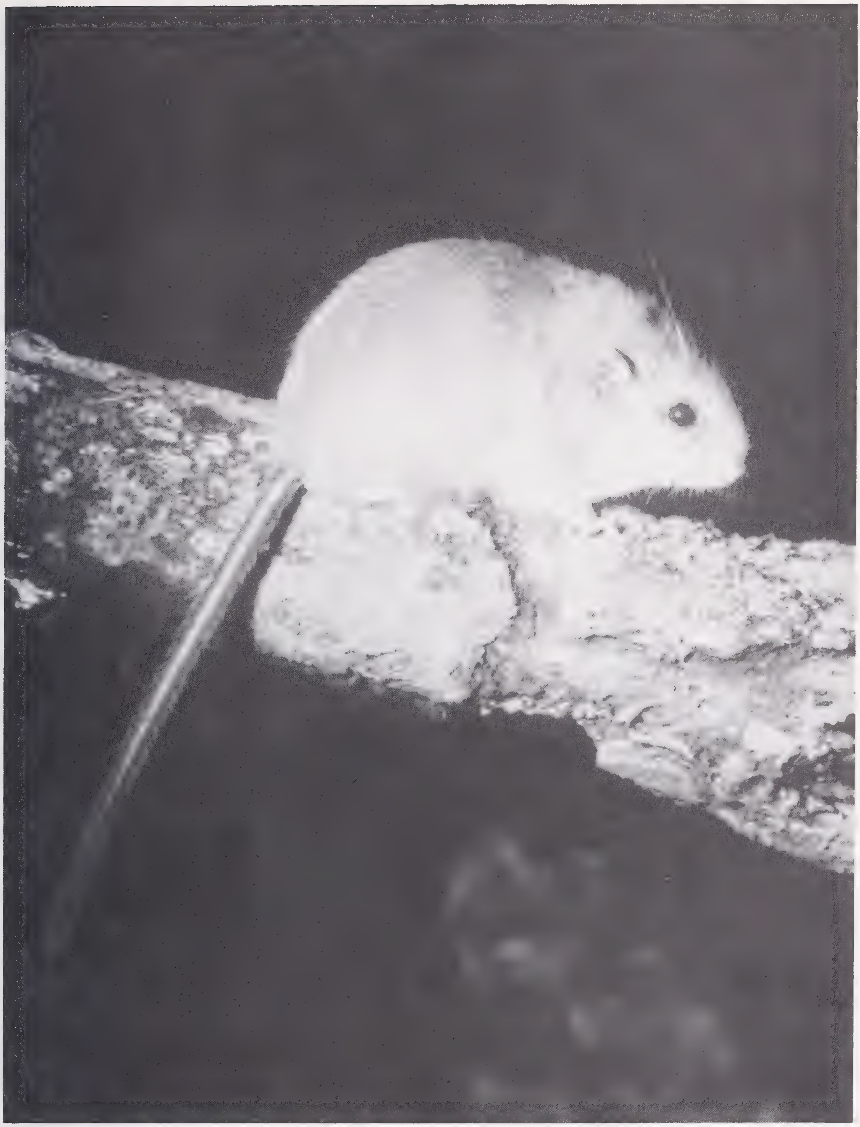


Fig. 92. Sumichrast's vesper rat, *Nyctomys sumichrasti. Photo by B. L. Clauson.*

Vesper rats may be common in the forest at La Selva, but they are seldom observed because of their nocturnal, arboreal habits. Fleming (1973) reported catching a Sumichrast's vesper rat at La Selva in primary forest. An adult and subadult were collected by Findley in the laboratory buildings in July 1974. An adult male captured on 7 August 1971 had fully scrotal testes measuring 14×7 mm.

Specimens examined (3)—Finca La Selva, 3 km S of Puerto Viejo [1 female, KU; 2 sex?, MSB]; 7.3 mi SE of Puerto Viejo [1 male, TTU].

Oryzomys albigularis
Tomes' Rice Rat, Ratón Arrocera

Tomes' rice rat occurs at high elevations in Costa Rica, Panama, Colombia, and Venezuela (Fig. 93). The Central American populations are restricted to elevations above 1,000 m in Costa Rica and the adjacent Chiriquí mountains of western Panama. A single subspecies, *Oryzomys albigularis devius*, is recognized in Costa Rica and western Panama. This northern disjunct population of *O. albigularis* is isolated by the Panamanian lowlands from the populations in extreme eastern Panama, Colombia, and Venezuela. Gardner (1983b) considered this disjunct population to be a distinct species, *Oryzomys devius*.

Tomes' rice rat previously was thought to be restricted in Costa Rica to the Cordillera Central and Cordillera de Talamanca. However, we recently have found this distinctive species to be abundant in the cloud forests above Monteverde in Puntarenas Province at 1,740 to 1,780 m, thus extending its known range into the Cordillera de Tilaran.

We observed Tomes' rice rat at two localities in Braulio Carrillo at elevations of 1,000 m and 2,050 m. They appear to be restricted to undisturbed forests. We suspect that the species is widespread and common in appropriate habitats. An adult female collected on 28 April carried three embryos (all in the right uterine horn) with crown-rump lengths of 28 mm. Four adult males had testes that measured 15×9 mm, 13×9 mm, 13×8 mm, and 13×7 mm in April. Subadult-sized animals were collected on 5–6 August 1967.

Specimens examined (8)—1.5 mi S of Cariblanco, 2,900 ft [1 male, 2 females, MVZ]; 3.5 km S, 11.5 km E of San Miguel, 1,000 m [1 male, FMNH; 1 male, UNA]; 5 km E of Vara Blanca, 2,050 m [1 male, 1 female, FMNH; 1 male, UNA].

Oryzomys alfari
Allen's Rice Rat, Ratón

Allen's rice rat is found from southeastern Honduras along the Caribbean lowlands to western Panama.

Three specimens of *Oryzomys alfari* are known from Heredia Province, two of which were captured at La Selva. Fleming (1973) reported that the specimens he collected were caught in live traps baited with corn and placed on the ground.

Specimens examined (2)—Finca La Selva, 3 km S of Puerto Viejo [2 females, UMMZ].

Additional record (1)—32 mi S of Puerto Viejo [1, LACM].

Oryzomys bombycinus
Long-whiskered Rice Rat, Ratón Arrocera

Long-whiskered rice rats are known from only two localities in the eastern Caribbean lowlands of Honduras and Nicaragua and from only a few additional localities in Costa Rica, Panama, western Colombia, and Esmeraldas Province of extreme northwestern Ecuador. The systematics and ecology of this poorly known mouse were reviewed by Pine (1971) and Jones and Engstrom (1986).

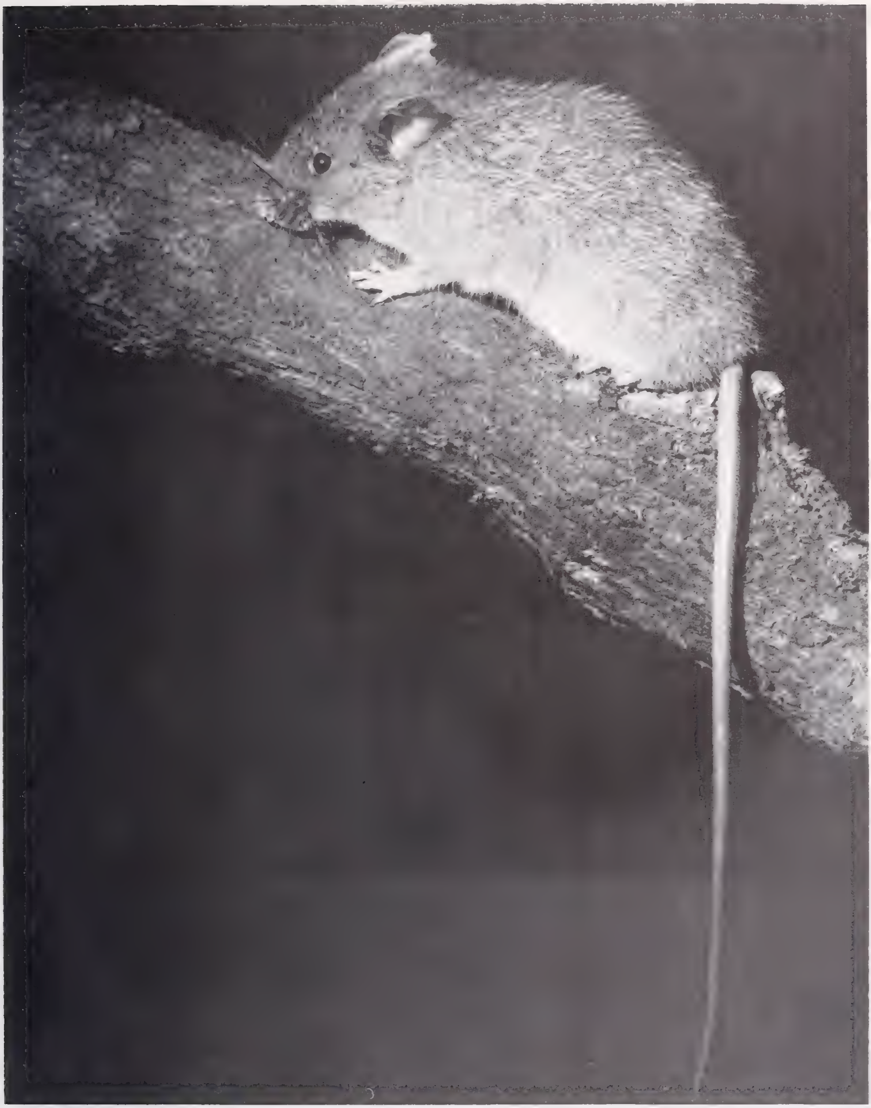


Fig. 93. Tomes' rice rat, *Oryzomys albigularis. Photo by B. L. Clauson.*

One young adult female captured on 7 April had two newly developed embryos in the right uterine horn. Testes measurements on four males captured in late March and early April were 12×6 mm, 10×5 mm, 9×5 mm, and 8×6 mm.

Specimens examined (7)—Finca La Selva, 3 km S of Puerto Viejo [2 males, UMMZ]; 11 km S, 4.5 km W of Puerto Viejo, 325 and 340 m [2 males, FMNH; 1 male, UNA]; 1 km S, 11.5 km E of San Miguel, 680 m [1 male, 1 female, FMNH].

Oryzomys caliginosus
Dusky Rice Rat, Ratón Arrocera

Dusky rice rats are found from extreme eastern Honduras and Nicaragua to western Ecuador (Fig. 94). In Costa Rica the subspecies *Oryzomys caliginosus chrysomelas* is found at lower elevations. The biology of dusky rice rats was reviewed recently by Gardner (1983b).

The mean litter size, as judged by counts of embryos and recent placental scars, of three females was 3.0 (Table 2). Mean testes length and width for nine adult male *O. caliginosus* was 10.2×5.8 mm.

A single adult female *Ixodes venezuelensis* was found on *O. caliginosus*.

Specimens examined (41)—Finca La Selva, 3 km S of Puerto Viejo [1 male, UMMZ]; Parque Nacional Braulio Carrillo [1 male, 1 female, UNA]; Puerto Viejo, Río Sarapiquí, 300 ft [5 males, 4 females, FMNH; 1 male, 1 female, LACM; 1 sex ?, UNA]; 1.7 mi S of Puerto Viejo [1 male, LACM]; 4.4 mi S of Puerto Viejo [1 male, LACM]; 5.7 mi S of Puerto Viejo [1 male, LACM]; 11 km S, 4.5 km W of Puerto Viejo, 260 and 280 m [7 males, 5 females, FMNH; 1 male, 2 females, UNA], 1 km S, 11.5 km E of San Miguel, 680 m [4 males, 4 females, FMNH].

Fig. 94. Dusky rice rat, *Oryzomys caliginosus. Photo by B. L. Clauson.*

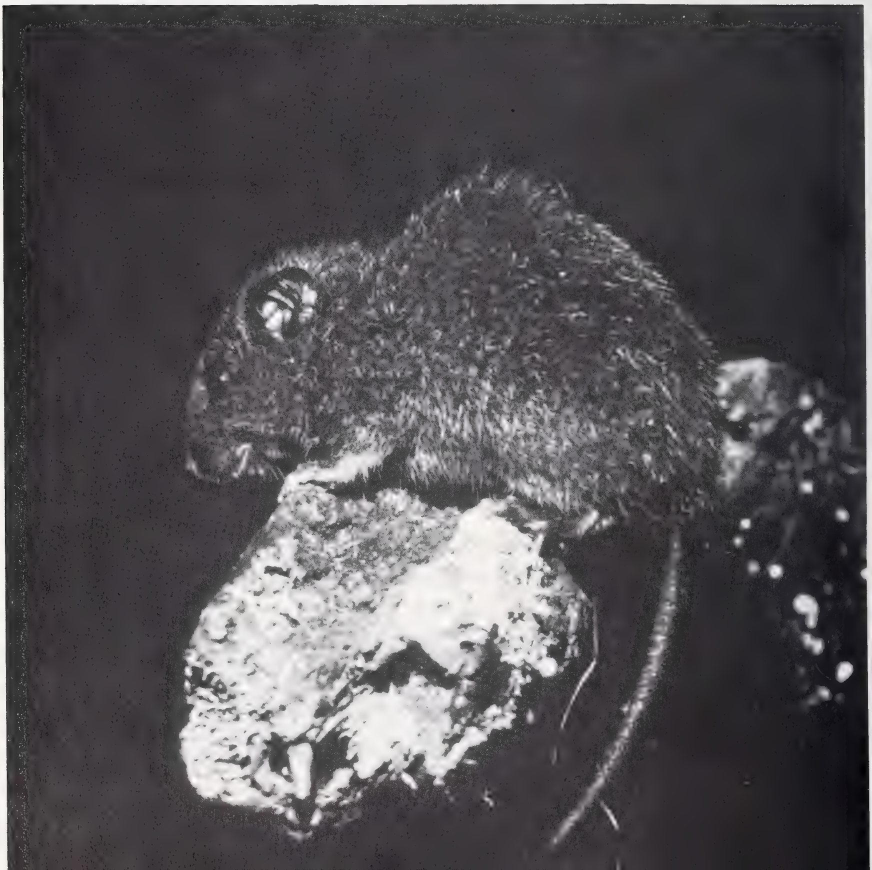


Table 2. *Reproductive characteristics of five adult (weight > 36 g) female* Oryzomys caliginosus *from Heredia Province, Costa Rica.*[a]

Date of capture	Reproductive characteristics
27 March 1986	numerous placental scars
28 March 1986	3 embryos (1L–2R)
30 March 1986	pubic symphysis open, mammae enlarged; released
8 April 1986	3 embryos × 24 mm (1L–2R)
10 April 1986	3 recent placental scars (2L–1R)

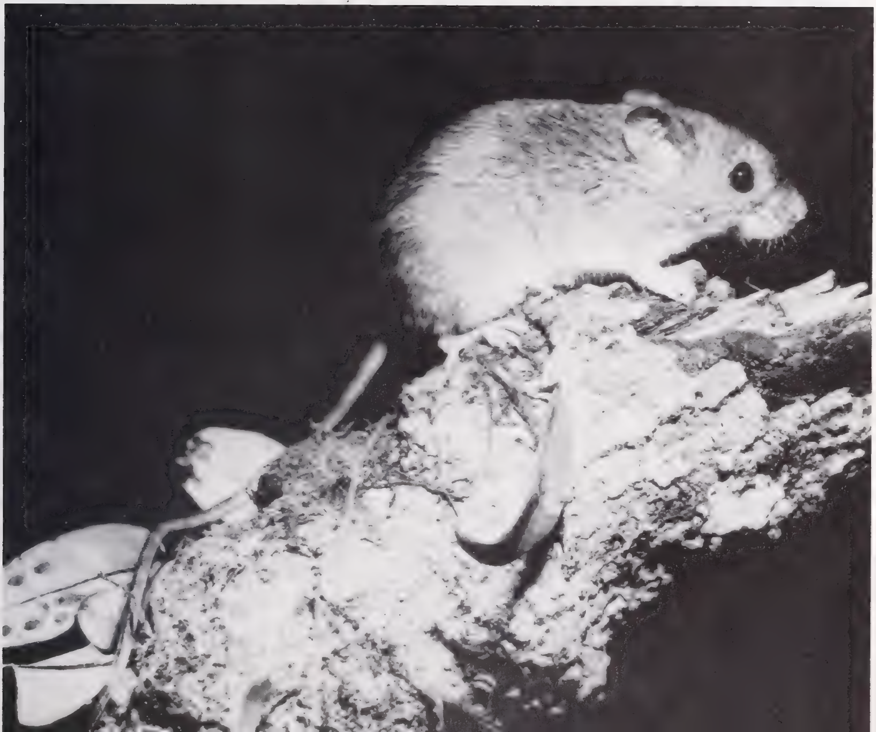
[a] Additionally, one female weighing 30.0 g had recently given birth; other females weighing 30, 32, and 36 g were nulliparous. Two females weighing more than 36 g were not reproductively active.

Oryzomys fulvescens
Pygmy Rice Rat, Ratón

Pygmy rice rats are found from central Mexico to eastern Panama (Fig. 95). Perhaps as many as four subspecies of *Oryzomys fulvescens* are found in Costa Rica, although the status of each of these taxa is in need of review. These subspecies include: *O. f. costaricensis*, *O. f. creper* (the subspecies occurring at La Selva), *O. f. pacificus*, and *O. f. vegetus*.

Pygmy rice rats are the smallest *Oryzomys* found in Costa Rica and among the smallest of all rodents found in the country. They are nocturnal and semiarboreal.

Fig. 95. Pygmy rice rat, *Oryzomys fulvescens. Photo by B. L. Clauson.*



Oryzomys fulvescens occupies a variety of habitats and a wide range of elevations from near sea level to 3,400 m. They are frequently trapped in open grassy and weedy habitats which suggests that they might be more abundant now in disturbed habitats than they were in pristine forests. In Nicaragua, Jones and Engstrom (1986) reported that pregnant females carried an average of four embryos, with a range of three to six.

Only three specimens of *O. fulvescens* are known from Heredia Province. A single adult female was obtained by E. H. Taylor along the Río Puerto Viejo on 6 August 1954 ''under a log,'' and a male and female were trapped south of Cariblanco in August 1967. We suspect that the few records from this region reflect a lack of concerted effort in searching for pygmy rice rats in appropriate habitats, and not that the species is rare.

Specimen examined (1)—Puerto Viejo River [1 female, KU].

Additional records (2)—1.5 mi S of Cariblanco [1 male, 1 female, MVZ].

Peromyscus nudipes
Cloud Forest Deer Mouse, Ratón

The systematic status of the white-footed mice and deer mice (genus *Peromyscus*) in Central America is in a state of flux (Fig. 96). Specimens of *Peromyscus* collected 5 km SE of Turrialba, Cartago Province, were regarded by Hall and Kelson (1959) and later by Hall (1981) as representing *Peromyscus mexicanus saxatilis*, whereas all other specimens from Costa Rica were regarded as representing a high-elevation species, *P. nudipes*, which was restricted to Costa Rica and adjacent Panama. In a revision of the *P. mexicanus* group, Huckaby (1980) reduced the name *nudipes* to a junior synonym of *P. mexicanus*. Thus, all *Peromyscus* within Costa Rica would represent the widespread species *P. mexicanus*, which, as Huckaby defined it, ranges from San Luis Potosí and Veracruz, Mexico, to western Panama. He recognized no subspecies within *P. mexicanus*, although he did state that there was considerable geographic variation. Huckaby's concept of the species *P. mexicanus* has not been supported universally by subsequent authors. The morphology of the Y chromosome of *nudipes* differs from *P. mexicanus* in that *nudipes* has a small metacentric Y, whereas in *P. mexicanus* the Y is a small acrocentric (Rogers et al. 1984; Smith et al. 1986). In both studies, *P. nudipes* was regarded as a distinct species.

The mean litter size, as judged by counts of embryos and recent placental scars of eight adult females, was 2.5 (Table 3). Mean testes length and width for 17 adult males was 15.1×8.5 mm.

Ticks collected from cloud forest deer mice include *Ixodes venezuelensis* (6 nymphs).

Specimens examined (46)—Barva, Sta. Lucia [2 males, 3 females, UNA]; 2 km N, 0.5 km E of Sacramento, 2,600 m [6 males, 3 females, UNA]; 1 km S, 11.5 km E of San Miguel, 710 m [3 males, 5 females, FMNH; 2 males, 1 female, UNA]; 3.5 km S, 11.5 km E of San Miguel, 750 and 1,000 m [7 males, 8 females, FMNH; 1 male, UNA]; 5 km E of Vara Blanca, 2,050 m [3 males, 2 females, FMNH].

Additional record (1)—1.5 mi W of Cariblanco [1 female, MVZ].

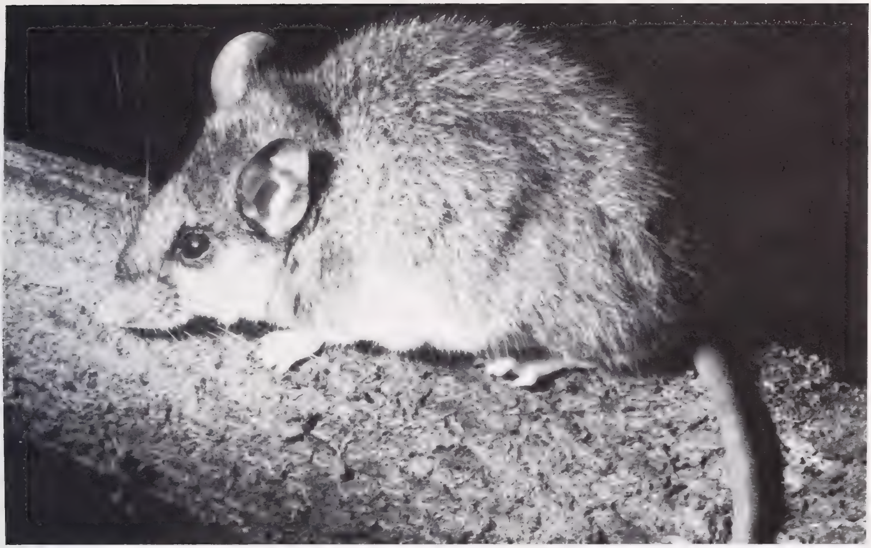


Fig. 96. Cloud forest deer mouse, *Peromyscus nudipes. Photo by B. L. Clauson.*

Table 3. *Reproductive characteristics of 10 adult (weight > 40 g) female* Peromyscus nudipes *from Heredia Province, Costa Rica.*[a]

Date of capture	Reproductive characteristics
4 April 1986	3 placental scars (2L–1R)
4 April 1986	2 embryos × 5 mm (1L–1R) plus old placental scars
5 April 1986	2 embryos × 12 mm (2R) plus old placental scars
5 April 1986	2 embryos × 6 mm (1L–1R)
7 April 1986	2 recent placental scars (1L–1R) plus old placental scars, lactating
8 April 1986	3 embryos × 8 mm (1L–2R)
8 April 1986	3 embryos × 8 mm (2L–1R)
8 April 1986	pregnant female; released
10 April 1986	3 recent placental scars (L), lactating
18 April 1986	uterus enlarged, lactating

[a] Additionally, two subadult females captured during this time period showed no sign of reproductive activity. All females weighing more than 40 g were reproductively active.

Reithrodontomys creper
Chiriquí Harvest Mouse, Ratón de la Cosecha

Chiriquí harvest mice have been reported from the Cordillera Central of Costa Rica, as far north as volcanos Irazú, Barva, and Poás, and southward through the Talamancas to the Chiriquí highlands of western Panama (Fig. 97). Recently, we have found *Reithrodontomys creper* to be abundant in the cloud forests above Monteverde, Puntarenas Province, thus extending the known range of the species farther north and west in Costa Rica into the Cordillera de Tilaran. Also, we have caught *R. creper* at San Gerardo de Dota, San José Province, at 2,600 m in pastures and in 5-year-old scrub that had been pasture. These are high-elevation mice; localities of capture range from 1,300 m near Angel Falls to more than 3,000 m. Although Chiriquí harvest mice are not uncommon in the appropriate habitat, at these higher elevations, rodents have not been studied intensively and little has been published on their biology. This species seems to prefer pristine forest as there have been few reports of it in second growth or disturbed habitats. There are no subspecies of *R. creper* recognized.

We encountered *R. creper* at 2,050 m in the park, and we suspect that it occurs throughout much of the higher-elevation forests of Braulio Carrillo. *Oryzomys albigularis*, *Peromyscus nudipes*, and *Scotinomys teguina* were the abundant small mammals encountered along with *R. creper* at this site. Two adult females collected on 17 and 20 April each carried three embryos, both had one embryo in the left uterine horn and two in the right. Embryos from one female had crown-rump lengths of 4 mm, those from the second had crown-rump lengths of 5 mm. A third adult female was not pregnant. Three adult males had testes that measured 19×10 mm, 19×9 mm, and 15×9 mm.

Specimens examined (5)—5 km E of Vara Blanca, 2,050 m [3 males, 2 females, FMNH].

Additional records (4)—Altos de Roble, S Fork Río Las Vueltas, 1,450 m [3, LACM]; 1.2 mi N of Angel Falls, 1,300 m [1, LACM].

Reithrodontomys rodriguezi
Rodriguez's Harvest Mouse, Ratón de la Cosecha

Reithrodontomys rodriguezi was described originally on the basis of two subadult specimens from Volcán Irazú, Cartago Province, at 9,400 ft (2,865 m) by Goodwin (1943). He described it as ''A moderately large harvest mouse with soft dense pelage, long unicolor tail, large ears and white underparts,'' and stated that the holotype was taken in long grass at the edge of rain forest (Goodwin 1943:1). For the next four decades the species was not encountered again and remained perhaps the most poorly known and enigmatic mammal of the country. Single specimens are now known from Asunción and Volcán Irazú, both in Cartago Province (McPherson 1985). The presence of *R. rodriguezi* on Volcán Barva was noted recently by Lumer and Schoer (1986), who felt that this was one of several species of rodents that pollinated flowers of *Blakea* sp.

We encountered *R. rodriguezi* at two localities on the northeastern slope of Volcán Barva during the 1986 expeditions. Specimens were taken at elevations

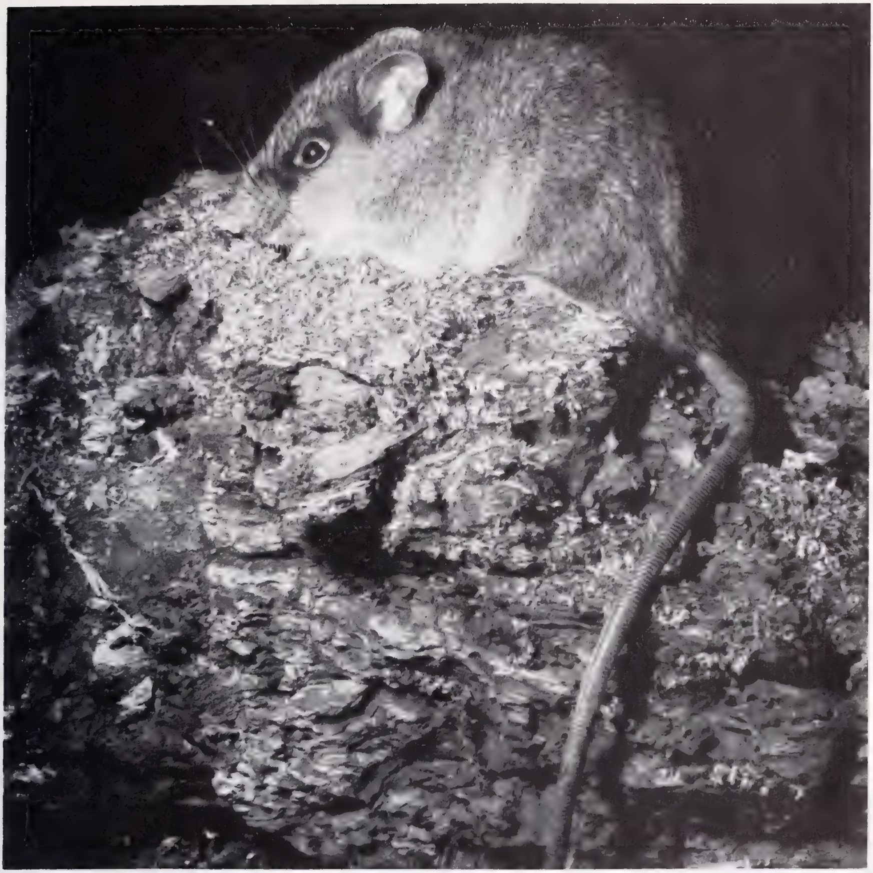


Fig. 97. Chiriquí harvest mouse, *Reithrodontomys creper. Photo by B. L. Clauson.*

ranging from 1,500 to 2,500 m.

Specimens examined (3)—Parque Nacional Braulio Carrillo, 2,500 m [1 female, UNA]; 9 km S, 11.5 km E of San Miguel, 1,500 m [2 females, KU].

Additional record (1)—Cerro Chompipe, Volcán Barva, 2,090 m [AMNH].

Mus musculus
House Mouse, Ratón de Casa

The house mouse was indigenous to the Old World, perhaps being found originally through much of central Asia from the Mediterranean to China. It is now a commensal that has followed humans throughout much of the world.

We captured only two house mice at 2,600 m during the survey. The adult female weighed 14.7 g, the adult male weighed 14.3 g and had testes measurements of 7×4 mm.

Specimens examined (2)—2 km N, 0.5 km E of Sacramento, 2,600 m [1 male, 1 female, UNA].

Scotinomys teguina
Alston's Brown Mouse, Ratón

Alston's brown mouse is found at higher elevations from southern Mexico to the Chiriquí mountains of western Panama (Fig. 98). Two subspecies of Alston's brown mouse occur in Costa Rica, *Scotinomys teguina irazu* throughout most of the mountainous regions of the country and *S. t. apricus* in extreme southern Costa Rica.

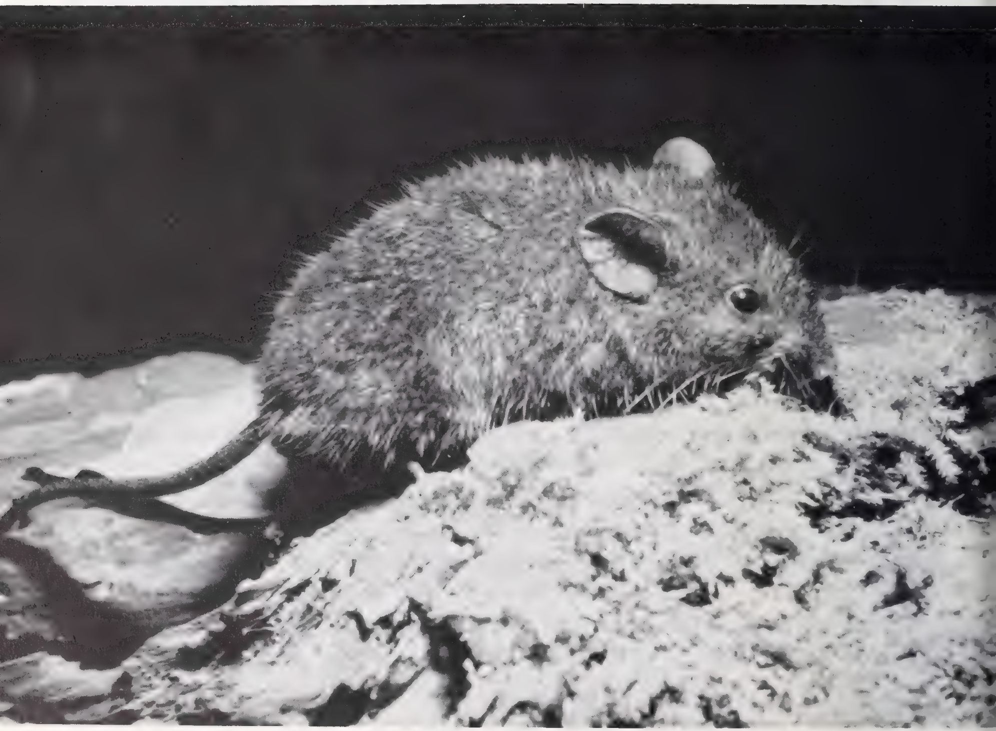
Scotinomys is an abundant rodent in a wide variety of habitats. It is apparently highly insectivorous and uses audible high-pitched vocalizations for intraspecific communication. Brown mice are active during daylight as well as at night.

We captured four adult females in mid-April. One carried two embryos in the left uterine horn with crown-rump lengths of 11 mm; one had four recent placental scars, three in the left uterine horn and one in the right; one was lactating; and one had no embryos. A juvenile male was captured on 13 April. *Scotinomys* was frequently captured during the day, attesting to the diurnal activity of these insectivorous rodents.

Specimens examined (17)—2 km N, 0.5 km E of Sacramento, 2,600 m [2 males, 2 females, UNA]; San José de la Montaña, Paso Llano, 1,800 m [1 male, 2 females, 3 unknown, KU]; 9 km S, 11.5 km E of San Miguel, 1,500 and 1,520 m [1 male, 3 females, FMNH; 1 female, UNA]; 5 km E of Vara Blanca, 2,050 m [1 male, 1 female, UNA].

Additional records (2)—1.2 mi N of Angel Falls [2, LACM].

Fig. 98. Alston's brown mouse, *Scotinomys teguina. Photo by B. L. Clauson.*

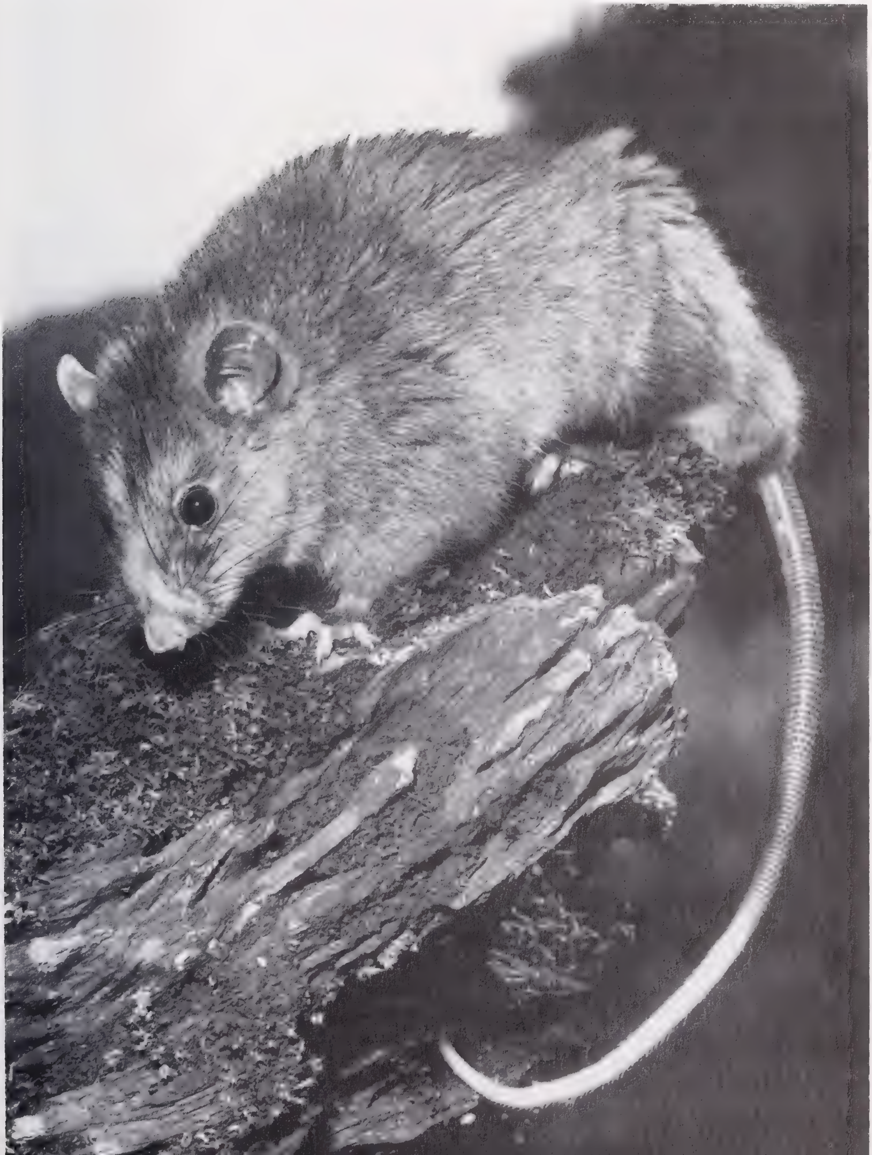


Tylomys watsoni
Watson's Climbing Rat, Rata Azul

Watson's climbing rat is found throughout much of Costa Rica and Panama, but has not been taken in adjacent countries (Fig. 99). No subspecies of *Tylomys watsoni* are recognized, and little is known of its ecology and habitat requirements. It is found from sea level to high elevation cloud forest.

Apparently, *T. watsoni* has been seen only once at La Selva. Fleming (1973) reported that one Watson's climbing rat was captured there by W. H. Freeland.

Fig. 99. Watson's climbing rat, *Tylomys watsoni. Photo by B. L. Clauson.*



Family Erethizontidae

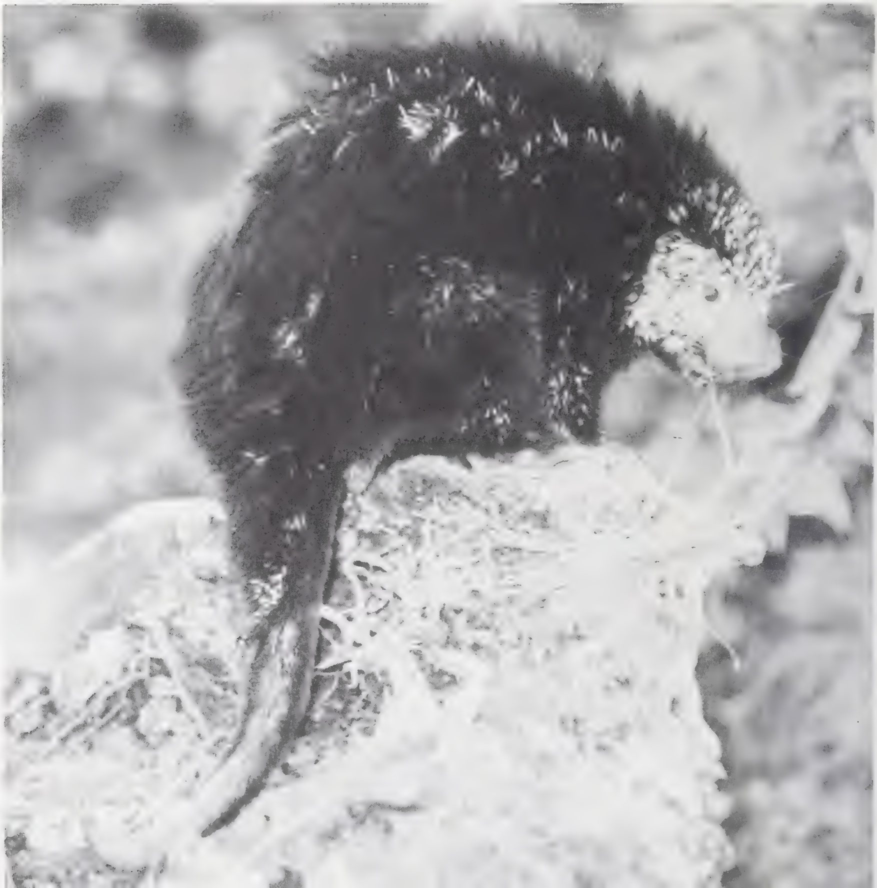
Coendou mexicanus
Prehensile-tailed Porcupine, Puercoespín

Prehensile-tailed porcupines are found from east-central Mexico to extreme western Panama (Fig. 100). The subspecies *Coendou mexicanus laenatus* is found throughout most of Costa Rica from sea level to about 3,000 m.

A prehensile-tailed porcupine was found dead along a road near the 2,050-m base camp; only bones and the distinctive hair remained. If the animal had been killed by hunters and the remains discarded there, it probably was taken in the general vicinity. Within Parque Nacional Braulio Carrillo, *C. mexicanus* was observed near the guard station at 2,600 m and near Laguna Barva at 2,700 m. Prehensile-tailed porcupines have been observed at La Selva on only five occasions: 1965, 9 March 1980, late July 1981, 23 November 1986, and May 1987. The biology of this species in Costa Rica was reviewed recently by Janzen (1983a).

Specimen examined (1)—Finca La Selva, 3 km S of Puerto Viejo [1 female, MNCR].

Fig. 100. Prehensile-tailed porcupine, *Coendou mexicanus. Photo by B. L. Clauson.*



Family Agoutidae

Agouti paca
Paca, Tepezcuintle

Pacas, the largest rodents in Costa Rica, are found from east-central Mexico south through all of Costa Rica and the northern two-thirds of South America to Paraguay, Uruguay, and southeastern Brazil (Fig. 101). Two subspecies are recognized in Costa Rica: *Agouti paca nelsoni* in the northwest Guanacaste region and *A. p. virgatus* throughout the rest of the country including La Selva. Due to their nocturnal, secretive nature, and because they are a highly prized and heavily hunted game species (Smythe 1983), they are rarely seen.

Pacas are common, but no longer abundant members of the La Selva fauna. They have been observed there year round. In June 1983, an adult and single juvenile were observed, and a lone juvenile was seen on 8 July 1988. In the past few years, sightings of pacas have increased at La Selva suggesting that the population is increasing. Pacas feed on the seeds of *Carapa guianensis* (Meliaceae), a common tree in swampy areas at La Selva, and they are one of the major vertebrate predators of these seeds (McHargue and Hartshorn 1983).

Pringle et al. (1984:198) reported ''We repeatedly saw tracks of *Agouti paca* (paca), and once found a hunters' blind with paca hair beneath it on a ridge above the Río Sardinalito'' in the Zona Protectora.

Family Dasyproctidae

Dasyprocta punctata
Agouti, Guatusa

Agoutis occur from southern Mexico to extreme northern Argentina (Fig. 102). Four subspecies of *Dasyprocta punctata* currently are recognized in Costa Rica (Hall 1981), with a single subspecies, *D. p. richmondi*, found throughout the Caribbean lowlands, mid- and high-elevation slopes. Agoutis are found in Costa Rica from sea level to high elevations; they occur at least as high as 2,400 m.

Agoutis are territorial and primarily monogamous; however, when abundant resources are available, a male may have two or more mates. Annually each mated female produces a single highly precocious young (Smythe 1983).

Agoutis are one of the most frequently observed mammals at La Selva. They are abundant in the primary forest and may be seen from the trails nearly every day. An adult and two young were seen in May 1981 and August 1983. Two were seen copulating in November 1982. In September 1982, an agouti was seen running from a small felid, probably a margay (*Felis wiedii*). Agoutis have been observed eating the fruits of *Dipteryx panamensis* and pejibaye palms, *Bactris gasipaes*, at La Selva. Vandermeer et al. (1979:19) reported that agoutis were observed eating the fruits of the palm *Welfia georgii*; the behavioral repertoire included ''picking up fruits from the ground, shucking them, eating the mesocarp and either eating the seed, dropping it to the ground, or burying it.'' Seeds of two other species of trees are heavily utilized by agoutis, *Carapa guianensis* and *Matisia ochrocalyx* (Bombacaceae). For all these tree species, agoutis may serve both as

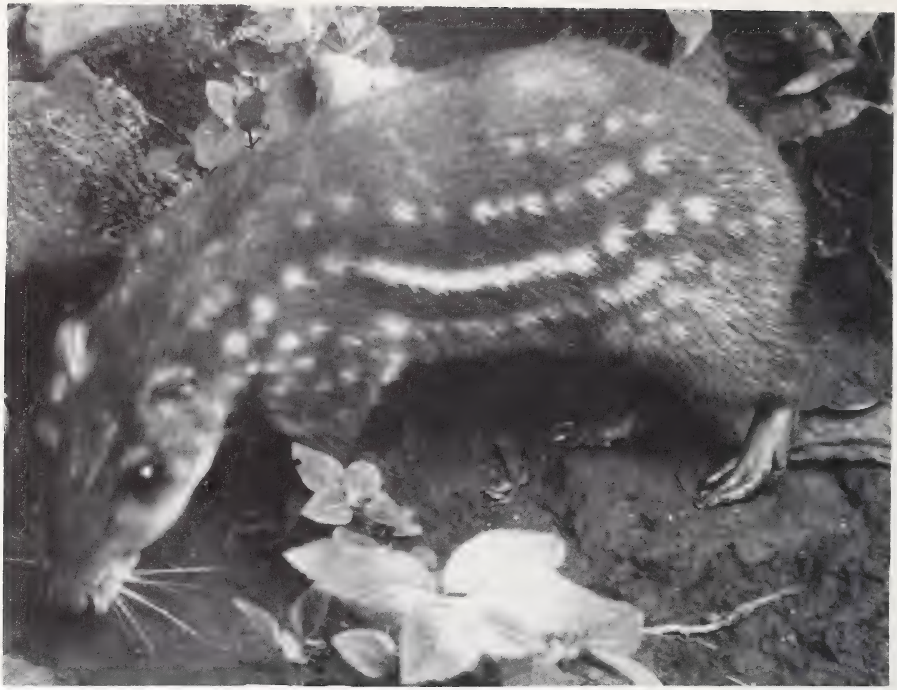


Fig. 101. Paca, *Agouti paca. Photo by R. M. Timm.*

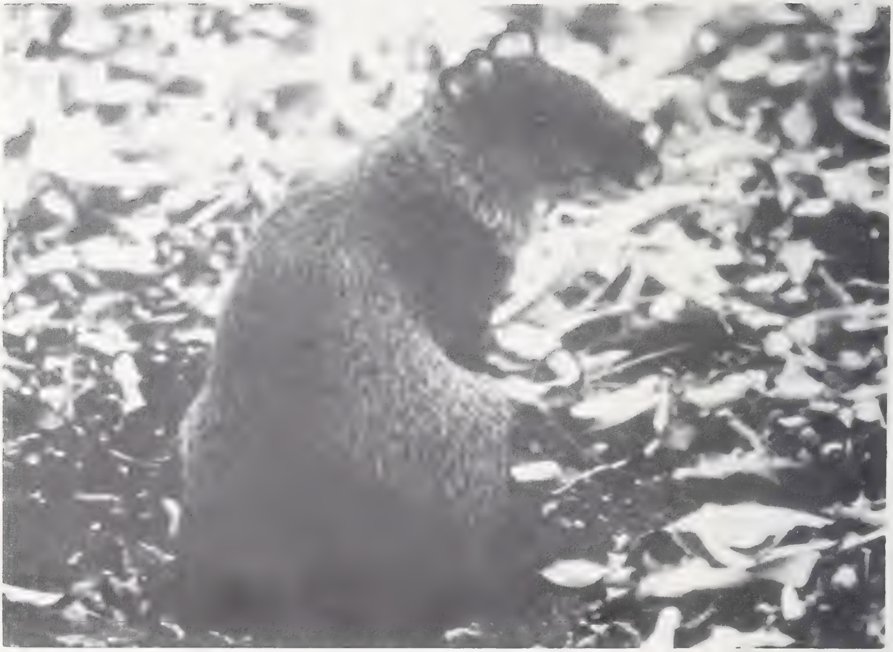


Fig. 102. Agouti, *Dasyprocta punctata. Photo by J. K. Adams.*

major vertebrate predators on the seeds and as principal dispersal agents, although Larson and Howe (1987) noted the lack of data on the actual effect of agoutis on specific species. One of the best places to observe agoutis at La Selva is the pejibaye grove.

Single agoutis were seen by members of our group at 100 m and 300 m within Parque Nacional Braulio Carrillo. The natural history of the agouti in Central America, based primarily on studies at Barro Colorado Island, Panama, was detailed by Smythe (1978).

Family Echimyidae

Hoplomys gymnurus
Armored Rat, Ratón

Armored or thick-spined rats are distributed from the Caribbean lowlands of extreme southeastern Honduras south through the tropical lowlands of Nicaragua, Costa Rica, and Panama to western Colombia and Ecuador. Two subspecies are known from Costa Rica, *Hoplomys gymnurus goethalsi* from southern Costa Rica and adjacent Panama and *H. g. truei* from central, eastern, and northern Costa Rica.

We obtained a single adult that was crossing a log over the Río Cantarrana at 280 m. Armored rats are certainly present at La Selva, although we know little of their abundance because they are rarely observed. Vandermeer et al. (1979) reported that they were able to capture *Hoplomys* in live traps using the fruit of the palm *Welfia georgii* as bait. They also noted that *H. gymnurus* readily consumed the mesocarp of *W. georgii* and would also eat the seeds if other foods were not available. It is likely that *H. gymnurus* and the closely related and similarly sized spiny rat, *Proechimys semispinosus*, are major food items of bushmasters.

Specimens examined (3)—Finca La Selva, 3 km S of Puerto Viejo [2 females, UMMZ]; 11 km S, 4.5 km W of Puerto Viejo, 280 m [1 female, FMNH].

Proechimys semispinosus
Tomes' Spiny Rat, Ratón

Tomes' spiny rat is widely distributed at lower elevations from southeastern Honduras and eastern Nicaragua through Costa Rica except in the northwest and along the western Andean lowlands of South America to southwestern Ecuador. Although the group is in need of revision, three subspecies of spiny rats are recognized from Costa Rica (Gardner 1983c): *Proechimys semispinosus rubellus* is known only from Pacuare, the type locality; *P. s. centralis* is found in northern Costa Rica with the exception of Guanacaste; and *P. s. panamensis* is found throughout the rest of the country. This species is captured occasionally at La Selva, although we know little of its biology in Central America. Greene (1988) reported that bushmasters prey primarily on spiny rats at La Selva.

Specimens examined (4)—Puerto Viejo, 100 m [1 male, KU]; Finca La Selva, 3 km S of Puerto Viejo [2 males, UMMZ]; 5.7 mi S of Puerto Viejo [1 female, LACM].

Additional record (1)—7.3 mi SE of Puerto Viejo [1 male, TTU].

ORDER CARNIVORA

Family Canidae

Canis latrans
Coyote

Coyotes are found from extreme northern Alaska and northwestern Canada across most of the United States, Mexico, and Central America to western Panama. A single subspecies of coyote, *Canis latrans dickeyi*, is found in Costa Rica. There is considerable controversy concerning the original distribution of coyotes in the country. It is documented in some of the earliest faunal reports that coyotes were abundant in Guanacaste Province and adjacent Nicaragua at the time of colonization by the Spanish and that the species is expanding its range in Central America (Monge-N. and Morera 1986, 1987). Vaughan (1983b) suggested that coyotes in Costa Rica originally were restricted to the tropical dry forests, and have rapidly expanded their range in Costa Rica and into Panama with the progress of recent deforestation. Coyotes in Costa Rica are opportunistic: in lowland dry Costa Rica they feed mostly on mammals, reptiles, and to a lesser degree on vegetation, birds, and arthropods (Janzen 1983b), whereas in the highlands the diet is almost exclusively mammals and birds (Vaughan and Rodriguez 1986).

During our 1986 expedition to Parque Nacional Braulio Carrillo, we found coyote scats in a pasture at 2,000 m, heard coyotes howling at 2,050 m, and observed their tracks at 2,600 m. There were no previous records of coyotes in the park.

Family Procyonidae

Bassaricyon gabbii
Olingo, Martilla

Olingos are found from central Nicaragua to western Colombia and Ecuador. Two subspecies are found in Costa Rica, the nominate race, *Bassaricyon gabbii gabbii*, in the south and *B. g. richardsoni* in the north. A second species, *B. lasius* is known from only the type locality at Estrella de Cartago in Cartago Province.

Olingos have been observed on a dozen occasions at La Selva. In August 1982 and again in July of 1988, single individuals were seen feeding on the fruits of *Cecropia*. Two individuals were observed together on 8 April 1988. Olingos are frequently misidentified as kinkajous.

Specimens examined (2)—Puerto Viejo, Río Sarapiquí, 300 ft [1 male, 1 female, UMMZ].

Nasua narica
Brown-nosed Coati, Pizote

Northern or brown-nosed coatis range from the southwestern United States through much of Central America to northwestern Colombia (Fig. 103). Coatis are extremely adaptable and are found in a wide variety of habitats including deserts, tropical dry forests, and tropical wet forests. The subspecies *Nasua narica narica* is found in Costa Rica from sea level to at least 3,500 m. Originally, coatis probably occurred in all natural terrestrial habitats in Costa Rica. The correct scientific name for the Central and South American coatis has varied over the years as several species and subspecies of *Nasua* have been described (Honacki et al. 1982). We concur with Decker (in litt.) in recognizing only two species of coatis; *Nasua narica*, the northern or brown-nosed coati in Central America, and *N. nasua*, the white-nosed coati, a widely distributed species in South America. The Cozumel Island coati is probably best considered as an endemic insular subspecies, *N. n. nelsoni*, of the Central American species.

Coatis are the most social of the procyonids. Adult males are solitary, but females and their offspring live in highly organized social groups. Coatis, unlike other procyonids, are active primarily during the day. They are omnivorous, consuming a wide variety of fruits, insects, and any smaller vertebrates that they are able to capture, including snakes, frogs, birds, bird eggs, and rodents. An excellent long-term study of the ecology and social behavior of coatis on Barro Colorado Island, Panama, was provided by Kaufmann (1962). The biology of coatis in Central America was reviewed recently by Kaufmann (1983).

In April 1986, we sighted lone coatis at 200 and 300 m in Parque Nacional Braulio Carrillo. Three coatis were seen together at 500 m, and the characteristic tracks of coatis were observed at 700 and 2,100 m. Coatis have been observed on numerous occasions at La Selva; there are records of sightings year round. The solitary adult males are seen most frequently. As many as 56 individuals have been seen in a group. Juveniles were observed in January, March, July, August, and September. They have been observed eating the fruits of *Dipteryx panamensis* and *Trophis racemosa*. In April 1986, we observed a group of 36 coatis eating the fruits of *Dipteryx*. Pringle et al. (1984) observed coatis in the Zona in January 1983.

Potos flavus
Kinkajou, Martilla or Mico de Noche

Kinkajous are found from tropical and subtropical southern Mexico through Central America to the Mato Grosso of Brazil (Fig. 104). The subspecies *Potos flavus chiriquensis* occurs throughout Central America to the Darién of Panama. A second Costa Rican subspecies, *P. f. arborensis*, was described by Goodwin (1938) for eastern Costa Rica; however, Kortlucke (1973) demonstrated that this subspecies was based on age-dependent characters and thus is not taxonomically valid.

There are numerous reports of kinkajous by researchers at La Selva. They have been found there year around. In April 1981, several kinkajous were observed

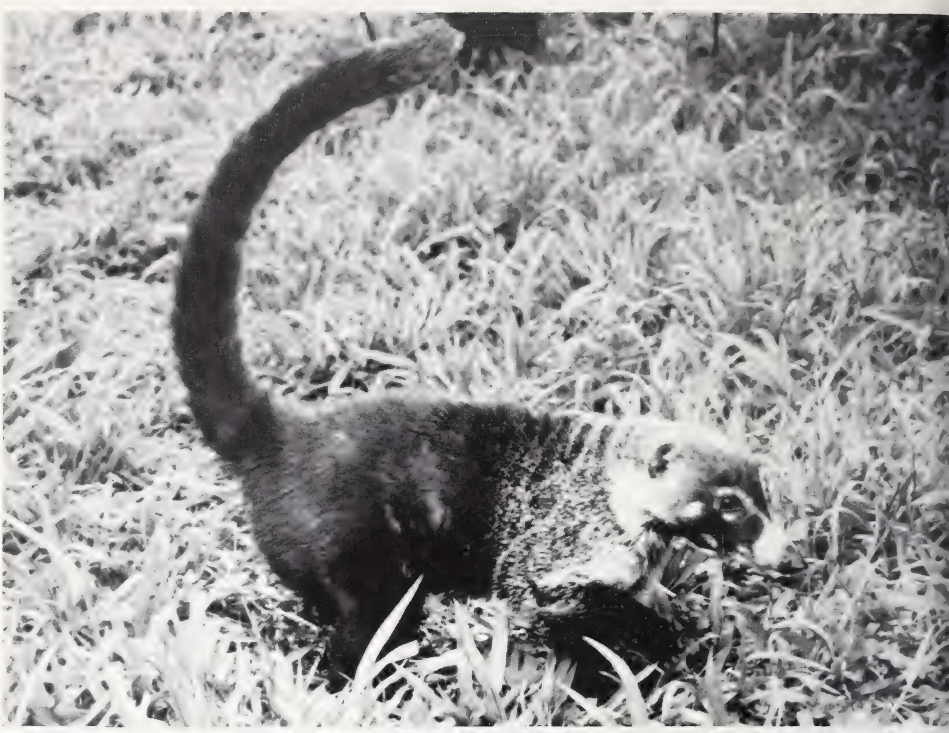


Fig. 103. Brown-nosed coati, *Nasua narica. Photo by R. M. Timm.*

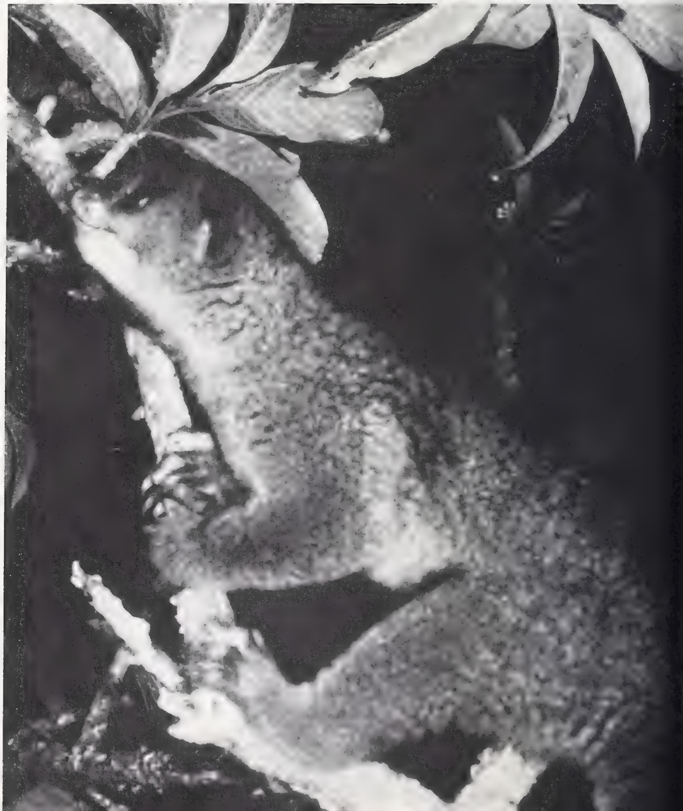


Fig. 104. Kinkajou, *Potos flavus. Photo by R. K. LaVal.*

feeding on the fruits of *Inga coruscans*. Three kinkajous were seen together on 9 July 1988. Kinkajous at La Selva were reported to shuck the fruits of the palm, *Welfia georgii*, eat the mesocarp, and drop the seeds to the ground (Vandermeer et al. 1979). Pringle et al. (1984) saw one kinkajou in the Zona Protectora in 1983. The biology of kinkajous was reviewed recently by Ford and Hoffmann (1988).

Additional records (1)—Puerto Viejo, Río Sarapiquí, 300 ft [1 female, MVZ].

Procyon lotor
Raccoon, Mapachín

Raccoons are found through North America and Central America from southern Canada to eastern Panama, with the exception of the most arid deserts and high elevations of the Rocky Mountains (Fig. 105). Two subspecies of *Procyon lotor* are found in Costa Rica, *P. l. crassidens* throughout most of the country and *P. l. pumilus* near the Panamanian border. A second species of raccoon, the crab-eating raccoon (*Procyon cancrivorus*), also occurs in the country; its known distribution is southwestern Costa Rica, extending as far north as Quepos on the Pacific coast.

Raccoons have been observed on only eight occasions at La Selva; six of these were lone individuals, but two animals were seen together twice. The most recent observation was in August 1987 of a single individual. This paucity of observations of animals as large and easily seen and identified as raccoons suggests that they are uncommon. The biology of raccoons was reviewed by Lotze and Anderson (1979) and in Costa Rica by Sanderson (1983).

Family Mustelidae

Conepatus semistriatus
Striped Hog-nosed Skunk, Zorro Hediondo

Striped hog-nosed skunks are found from Veracruz, Mexico, eastward along the Caribbean coast of Central America to western Panama. The Costa Rican subspecies, *Conepatus semistriatus trichurus*, is probably found throughout the country but is observed infrequently. Where hog-nosed skunks are common, such as the Monteverde area, they are frequently killed along roadways by passing vehicles.

Hog-nosed skunks are insectivorous-omnivorous terrestrial foragers. They are one of the most strictly noctural of the Neotropical carnivores. As most observations of these skunks have been of single individuals, we assume that they are solitary.

A striped hog-nosed skunk was observed foraging at the 700-m base camp along the Río Cascante on two consecutive evenings and one was seen near the 2,600-m base camp in late April. There are 23 observations of striped hog-nosed skunks at La Selva from 1979 through mid-1988. Judging from the close proximity in time and area, these sightings probably represent repeated sightings of few individuals. In recent years, one individual has been seen almost every evening at dusk near the visitor center, in the adjacent second growth, and occasionally on the Río Puerto Viejo bridge.

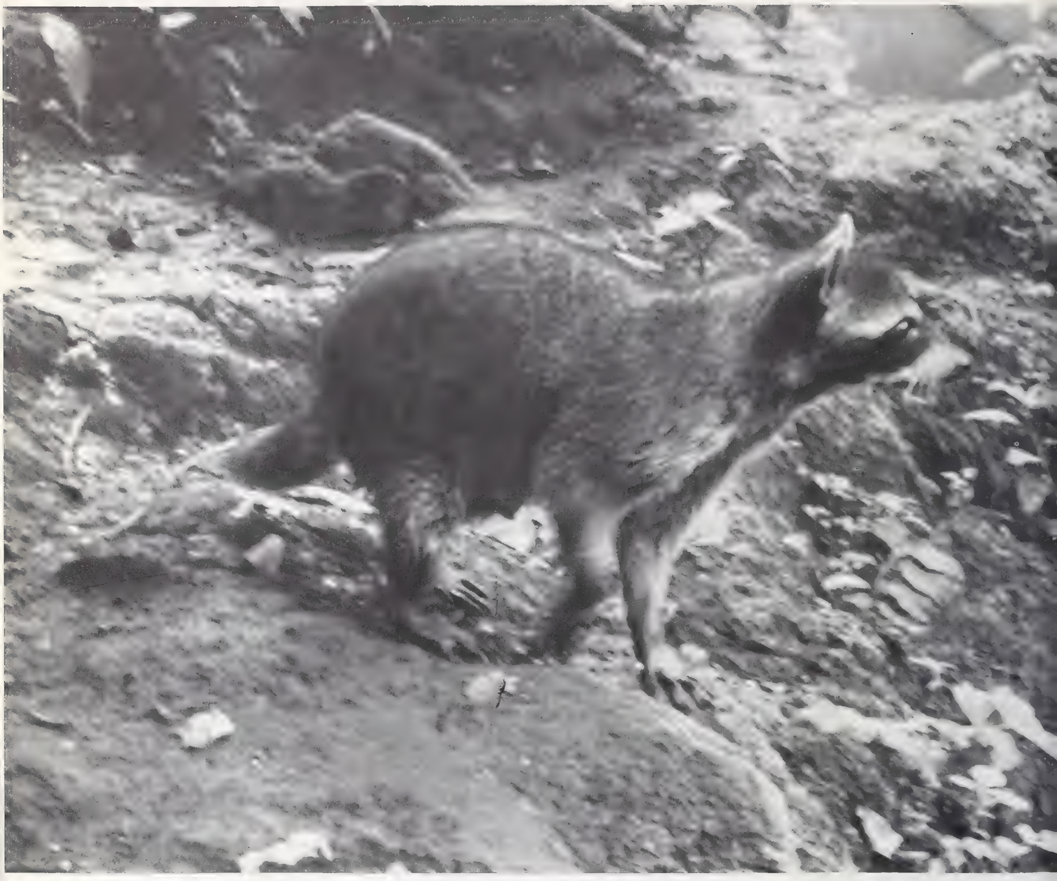


Fig. 105. Raccoon, *Procyon lotor. Photo by R. M. Timm.*

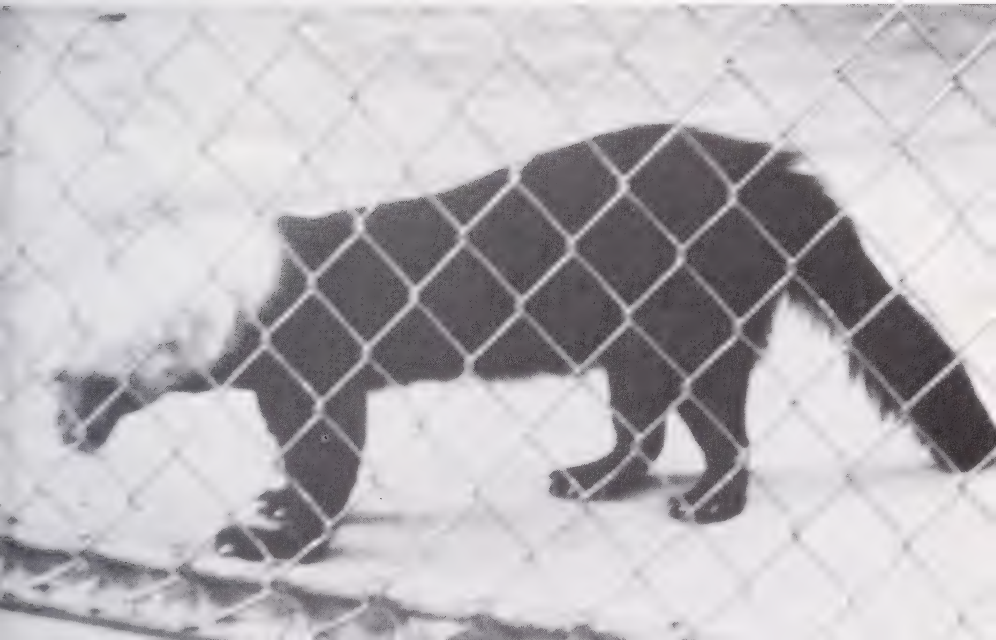
Eira barbara
Tayra, Tolomuco or Gato de Monte

Tayras are found from Sinaloa and Tamaulipas, Mexico, south to northern Argentina (Fig. 106). Two subspecies are known from Costa Rica: *Eira barbara biologiae* from the southern and eastern part of the country and *E. b. inserta* from northern and western Costa Rica. Tayras are found from sea level to high-elevation cloud forest.

Tayras are the most arboreal and diurnal of the Neotropical mustelids. They are strong and agile climbers and frequently are seen during the day moving through the tree tops as well as on the ground. They eat small rodents, reptiles, and fruits, especially figs (*Ficus*). The biology of tayras in Costa Rica was reviewed recently by Janzen (1983c).

Tayras have been observed on several dozen occasions at La Selva. There are records of sightings from throughout the year. Judging from their close proximity in time and space, these records probably represent a few individuals seen repeatedly. Most sightings have been of lone animals. However, on 4–5 April 1982, an adult and a single young were observed together. Two observations are of two individuals together; three were observed together twice, and once five were seen together (14 June 1987). Many of the observations were made near buildings or on trails frequently traveled by researchers. Several sightings near El Sura in January 1987 were probably of the same individual. Hartshorn (in litt.) saw an adult and three juveniles in the pejibaye grove at La Selva in the early 1970's. A member of our group saw a tayra on two occasions near the 2,050-m camp in Braulio Carrillo, and another was seen at 200 m.

Fig. 106. Tayra, *Eira barbara. Photo by R. M. Timm.*



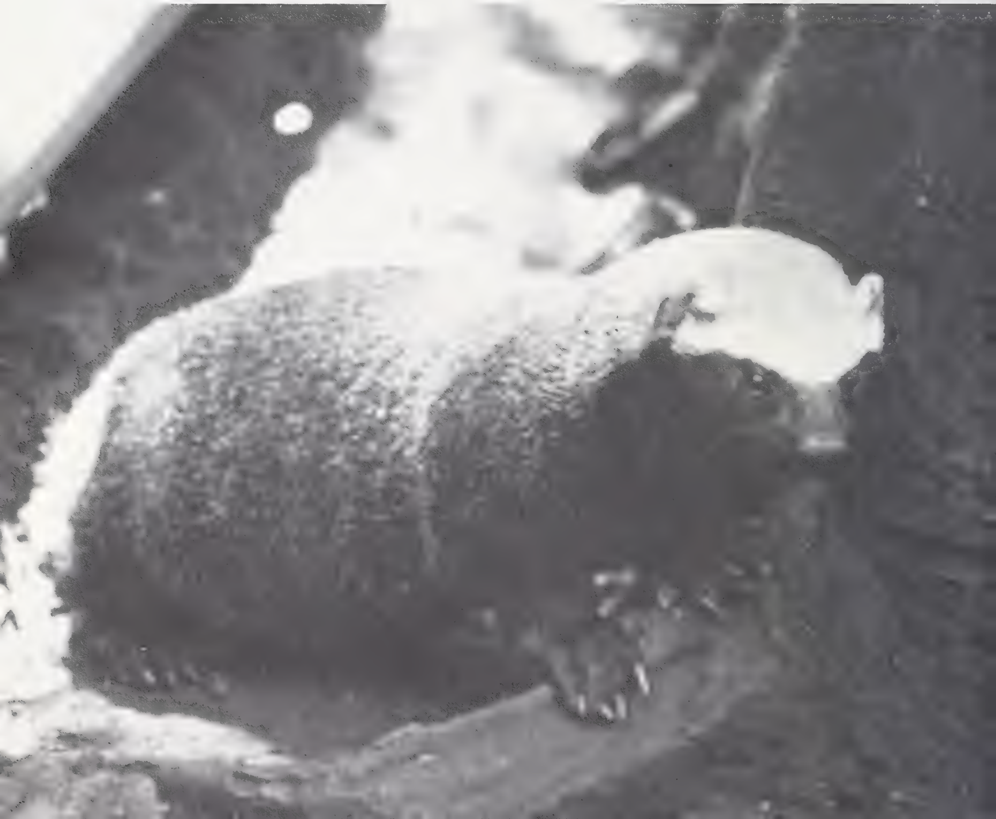
Galictis vittata
Grison, Grisón or Tejón

Grisons are found at lower elevations from central and eastern Mexico throughout Central America to Peru and southern Brazil (Fig. 107). The subspecies *Galictis vittata canaster* is found in Costa Rica from sea level to perhaps over 1,500 m. Most records of grisons are from below 500 m. In Costa Rica, however, grisons appear to be absent from the tropical dry forests of northwestern Costa Rica. They are uncommon and rarely observed throughout their range. Grisons should receive complete protection in Costa Rica as an endangered species.

Galictis vittata is found in a wide variety of habitats including both wet and dry tropical forests, open and wooded grasslands, and cultivated areas. Grisons are most often found near streams and rivers, and they swim readily. They are opportunistic predators and are known to prey on a variety of small mammals, including *Didelphis* and *Sigmodon*, lizards, snakes, frogs, and birds. Grisons are primarily nocturnal, although their activity may continue through the morning.

Grisons have been observed on nine occasions at La Selva. Although we have no record of this species from Braulio Carrillo, we expect that it occurs there.

Fig. 107. Grison, *Galictis vittata. Photo by R. M. Timm.*



Lutra longicaudis
Southern River Otter, Perro de Agua or Nutria

Southern river otters are found from northwestern Mexico south through Central America to Peru and Uruguay. All otters in Costa Rica are now considered as belonging to the subspecies *Lutra longicaudis annectens*; however, there are few actual records for the country. A specimen collected by C. Underwood from Río Grande, Villa Colón, San José Province, was described by Cabrera (1924) as a distinct species, *L. mesopetes*. River otters are included on Costa Rica's listing of Rare and Endangered Species.

We found fresh otter scat on a rock in the Río Cantarrana at 300 m; it contained the remains of crustaceans. Otters have been seen regularly at La Selva, primarily along the Río Puerto Viejo, Río Sarapiquí, and Quebrada El Salto. The 36 separate recordings of otters at La Selva (all but 5 have been of lone animals) include every month of the year. On several occasions in January 1987 and August 1988 we sighted two adult-sized individuals from the bridge over the Río Puerto Viejo. There is an otter den in the bluff of the Río Puerto Viejo about 300 m upstream from the station landing at La Selva.

Mustela frenata
Long-tailed Weasel, Comadreja

Long-tailed weasels are found from southern Canada through Central America to northern South America and along the Andes south to Bolivia (Fig. 108). The subspecies *Mustela frenata costaricensis* was described from San José, Costa Rica, and is now considered the subspecies that occurs throughout the country. There is little known about the distribution or ecology of weasels in Costa Rica. Long-tailed weasels are abundant at middle and high elevations including the Monteverde area. The taxonomy of this weasel was last reviewed by Hall (1951).

Long-tailed weasels have been sighted on only three occasions at La Selva. In 1970, Wilson and Janzen captured one just west of Braulio Carrillo; Janzen kept it in captivity for several months. Near the city of Heredia we have observed long-tailed weasels crossing roads between abandoned fields and in coffee plantations.

Family Felidae

Felis concolor
Mountain Lion, Puma or León de Montaña

Mountain lions are one of the most widely distributed mammals, originally found from Alaska across most of North America and throughout Central America and South America to Tierra del Fuego (Fig. 109). The subspecies *Felis concolor costaricensis* is distributed throughout Costa Rica but in reduced numbers because of hunting pressure. Mountain lions are rare in Costa Rica, although they are found in a variety of habitats from sea level to 3,300 m. Mountain lions are included on both the Costa Rican and U.S. Rare and Endangered Species lists. The ecology of mountain lions, primarily based on studies in North America, was reviewed recently by Currier (1983).

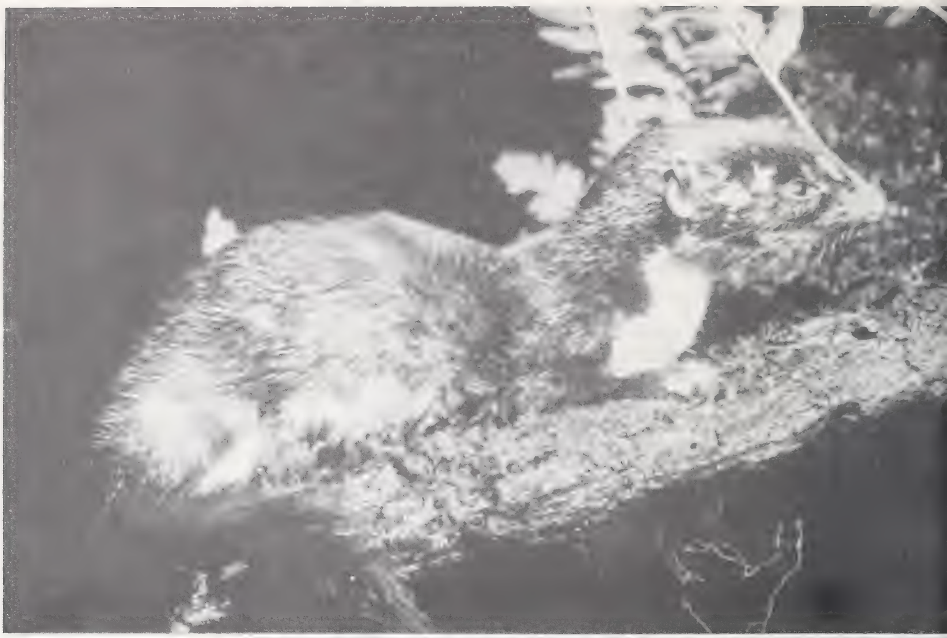


Fig. 108. Long-tailed weasel, *Mustela frenata. Photo by B. L. Clauson.*

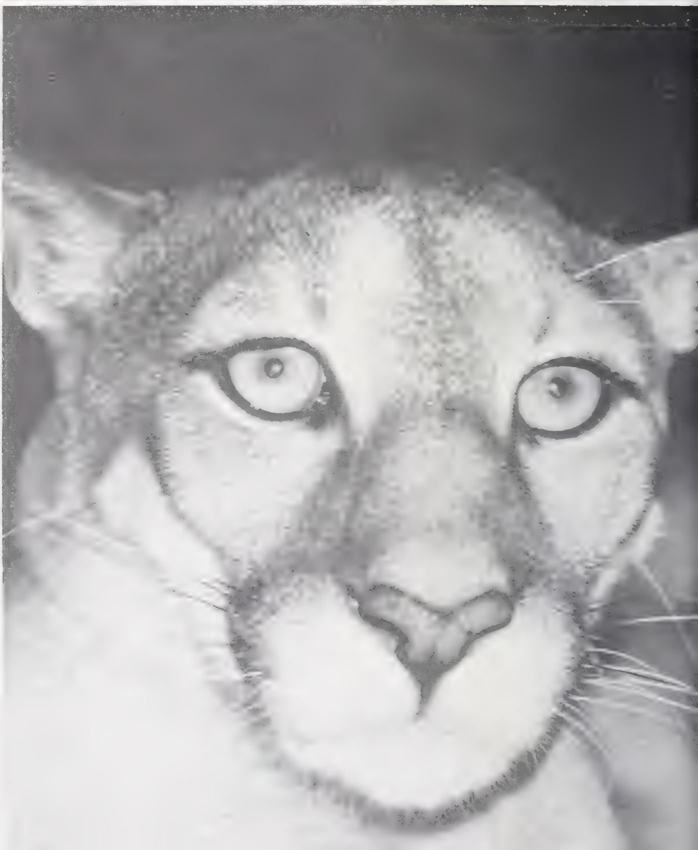


Fig. 109. Mountain lion, *Felis concolor. Photo by R. K. LaVal.*

An adult mountain lion was seen crossing a trail near the Magsaysay guard station at 200 m in January 1986 by Reinaldo Aguilar Fernández, a park guard. A second mountain lion was seen at 1,000 m by a group on 21 February 1987. Mountain lions have been observed on 12 occasions at La Selva. On one of these occasions, two adult-sized animals were sighted together. Hartshorn (in litt.) observed three mountain lions in Parque Nacional Braulio Carrillo along the Río Patria in 1986.

Specimen examined (1)—Moravia, Finca Tomás Guardia [1 male, UNA].

Felis onca
Jaguar, Tigre

Jaguars historically were found as far north as the Grand Canyon and California in the United States, through Mexico, all of Central America, and much of South America to northern Argentina (Fig. 110). In Costa Rica, the subspecies *Felis onca centralis* was once found from sea level to the higher forested elevations, although now its numbers and distribution have been reduced by hunting pressure and habitat destruction (Koford 1983a). Jaguars are included on both the Costa Rican and U.S. endangered species lists.

Jaguars are the largest terrestrial predators in the Neotropics. In Belize, armadillos, pacas, and brocket deer composed 94% of the diet of these nocturnal felids, although a wide variety of medium-sized mammals is consumed. There is extensive range overlap between males and females, but individuals are spaced within the territory to avoid contact with conspecifics except during the mating season. Males apparently use a small area for up to 2 weeks before shifting to another area (Rabinowitz and Nottingham 1986).

Jaguars have been seen eight times at La Selva. On several occasions, Vaughan tried unsuccessfully to capture and translocate a jaguar that had been killing livestock around Puerto Viejo since 1986. The local residents believe that it lives in La Selva. They have been seen at La Selva with increasing frequency in recent years. We found numerous large scats that we presume to be from a jaguar near the 2,050-m camp. At La Selva we have twice identified the remains of tamanduas in the scats of jaguars, although sloths and green iguanas are the primary prey items found in jaguar scats there (Greene and Losos 1988). Park guards reported to us that a jaguar was observed just before our 1986 expedition at 200 m within the park. In the Zona Protectora, Pringle et al. (1984:198) reported that "We repeatedly encountered tracks of *Felis onca* (jaguar) throughout the ZP [Zona Protectora], and a fresh scat was observed on the trail east of the base camp."

Felis pardalis
Ocelot, Manigordo or Ocelote

Ocelots are found from the southern United States along the Pacific and Caribbean coasts of Mexico through much of Central America to northern Argentina. The subspecies *Felis pardalis mearnsi* is found in Costa Rica. Ocelots occur in a variety of habitats including dense forest, second growth, and agricultural areas,

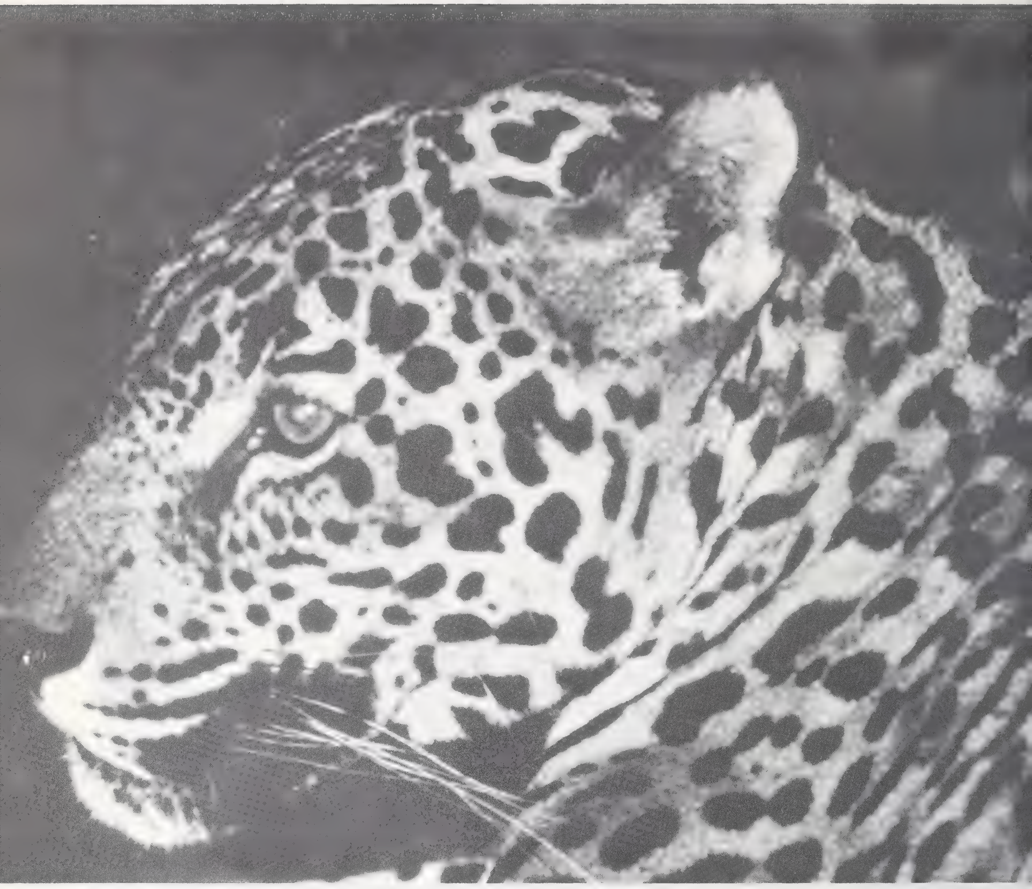


Fig. 110. Jaguar, *Felis onca. Photo by R. K. LaVal.*

where they range elevationally from sea level to nearly 3,800 m. Ocelots are included on both the Costa Rican and U.S. listings of endangered species. Ocelots and jaguarundis are the most frequently observed native felids in Costa Rica.

Ocelots are primarily nocturnal and are not infrequently crepuscular. They eat a wide variety of small and medium-sized mammals, reptiles, and birds. Spiny rats (genus *Proechimys*), often abundant rodents in an area, are caught and eaten frequently by ocelots. In Peru, Emmons (1988) found that males and females were solitary and occupy distinct territories that are maintained by scent marks. Adult females had nonoverlapping home ranges as did males. Male territories, however, overlapped those of three or more adult females.

We observed the tracks or scats of ocelots at 760 m, 2,000 m, and at 2,610 m within Parque Nacional Braulio Carrillo. Ocelots have been observed at La Selva on 17 occasions.

Felis wiedii
Margay, Caucél

Margays originally were found from the southwestern United States through Central and South America to northern Argentina (Fig. 111). The subspecies *Felis wiedii nicaraguae* formally occurred throughout Costa Rica from sea level to the higher elevations (Koford 1983b). Margays are included on both the Costa Rican and U.S. listings of endangered species.

Margays are arboreal predators. In Belize, M. J. Konecny (in litt.) found that the diet of this diminutive cat was primarily smaller arboreal rodents.

Margays have been seen at La Selva on only three occasions, in February 1982, in June 1986, and in March 1988.

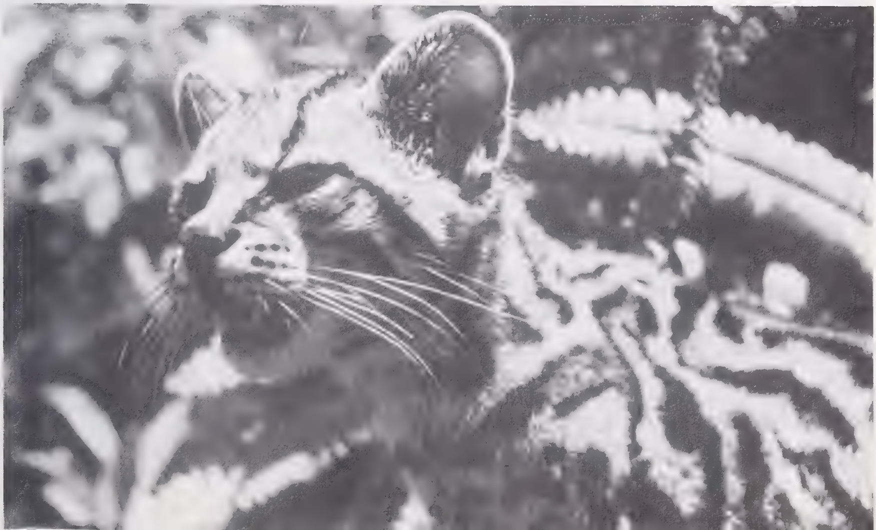
Felis yagouaroundi
Jaguarundi, León Breñero or Gatillo de Monte

Jaguarundis originally ranged from the southwestern United States through Central America to northern Argentina. The subspecies *Felis yagouaroundi panamensis* is distributed throughout Costa Rica in suitable habitat along both coasts to 2,000 m in elevation. Jaguarundis are one of the smallest and most variably colored felids in this region, with color phases ranging from grays and deep reddish-browns to blacks. Jaguarundis are included on both the Costa Rican and U.S. listings of endangered species.

Jaguarundis are perhaps the most diurnal of the Neotropical cats, and they are also the most adaptable, occurring in primary and secondary forests as well as in pastures. Small mammals, especially *Sigmodon* spp. and birds, made up most of the prey items of jaguarundis in Belize (Konecny, in litt.).

Jaguarundis have been observed at La Selva on 25 occasions with records from most months. An adult with four kittens was seen in July 1985. An adult was observed stalking a spiny rat on the Sura bridge in February 1983.

Fig. 111. Margay, *Felis wiedii. Photo by R. K. LaVal.*



ORDER PERISSODACTYLA

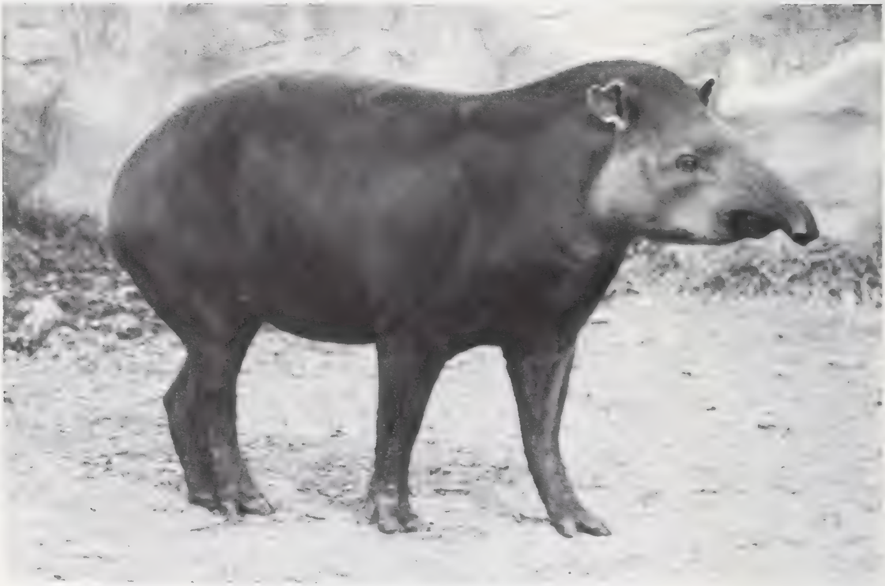
Family Tapiridae

Tapirus bairdii
Baird's Tapir, Danta

Baird's tapir (*Tapirus bairdii*) originally was found from southern Mexico east of the Isthmus of Tehuantepec south throughout Central America to the western slopes of the Andes in Colombia and Ecuador to the Gulf of Guayaquil (Fig. 112). Tapirs probably were common throughout most of Costa Rica before contact by Europeans. There are no recognized subspecies of Baird's tapir. In Costa Rica, tapirs are found in a wide variety of habitats from sea level to 3,800 m. They seem to require large tracts of primary forest and protection from hunting pressure in order to maintain adequate population levels (Janzen 1983d). Baird's tapir is included on both the Costa Rican and U.S. listings of rare and endangered species. The biology of tapirs in northwestern Costa Rica was investigated by Williams (1984).

We observed tapir tracks and droppings at several localities within Parque Nacional Braulio Carrillo, ranging from 100 to 2,000 m in elevation. Tracks were most common in the elevational range from 1,500 to 2,000 m. A single individual was observed at 1,800 m in February 1987. Tapirs were reported by Pringle et al. (1984) from the southern end of the Zona Protectora at 700 m in January 1983. Tapir tracks are seen regularly at La Selva, but the animals are rarely observed; most have been seen near the south end of the property. Slud (1960) implied that tapirs were common there in the late 1950's.

Fig. 112. Baird's tapir, *Tapirus bairdii*. *Photo by B. L. Clauson.*



ORDER ARTIODACTYLA

Family Tayassuidae

Tayassu pecari
White-lipped Peccary, Chancho de Monte

White-lipped peccaries once occurred in lowland tropical forests from Veracruz and Oaxaca in southern Mexico through Central America and much of tropical South America to Entre Ríos in northern Argentina (Fig. 113). One subspecies, *Tayassu pecari spiradens*, is found in Costa Rica; the type locality for this subspecies is Sipurio, Río Sixaola, Limón Province. This species is a wilderness species and endangered in Costa Rica due to overexploitation and habitat destruction (Vaughan 1983a). It is found from sea level to 1,500 m. There has been little work on white-lipped peccaries in Costa Rica, in part because they are now so rarely encountered. The ecology of this species recently was reviewed by Mayer and Wetzel (1987).

Between 1979 and 1987, herds of white-lipped peccaries have been recorded at La Selva on only five occasions, the most recent of these in July 1983. Pringle et al. (1984:198) reported, ''Local people told us that white-lipped peccaries (*T. pecari*) were especially vulnerable to overhunting because of large herd size and aggressive temperament, and that this species is now very rare or absent in the ZP [Zona Protectora].'' McHargue and Hartshorn (1983:401) stated of *T. pecari* in the La Selva area that ''According to knowledgeable local people, white-lipped peccaries are usually found in swamps feeding on *Carapa* seeds. We did not observe any sign of white-lipped peccaries in the Study Area II during the summers of 1974, 1975, and 1976.'' White-lipped peccaries apparently were abundant in the La Selva area as late as the early 1960's. Paul Slud (1960:76) wrote ''Ominous are the clopping, champing noises of a herd of White-lipped Peccaries; unsettling is the heavy, growling 'woof' of a startled individual close at hand.''

Although white-lipped peccaries have been given complete protection as an endangered species in Costa Rica, the species is still hunted in some areas.

Tayassu tajacu
Collared Peccary, Saíno

Collared peccaries are found from the southwestern United States throughout Central America and tropical South America south to Santiago del Estero in northern Argentina (Fig. 114). One subspecies, *Tayassu tajacu crusnigrum* is found in Costa Rica from sea level to about 3,000 m. Collared peccaries are one of the most important game species in Costa Rica.

Collared peccaries are common, obvious elements of the La Selva fauna; they have been seen there on numerous occasions year round. They have been observed in herd sizes of 25–30 individuals. Juveniles have been seen in May and July. The January 1983 and the 1986 expeditions into Braulio Carrillo recorded peccary tracks at numerous elevations. Although the tracks could not be identified to species, it

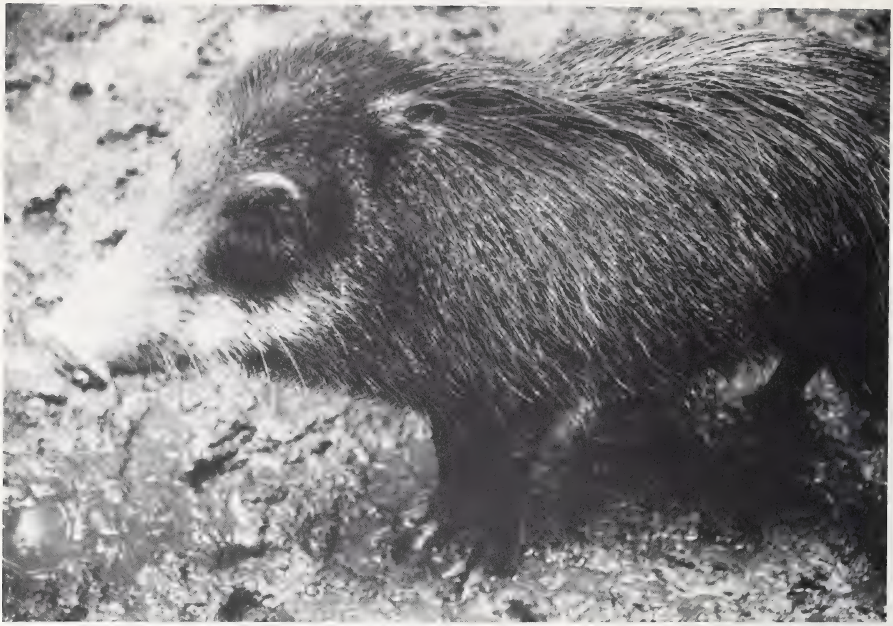
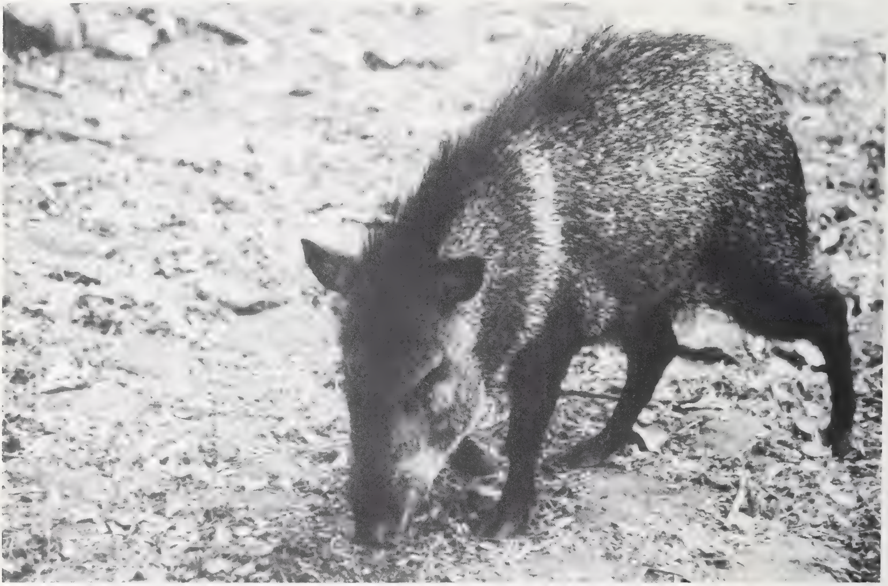


Fig. 113. White-lipped peccary, *Tayassu pecari. Photo by B. L. Clauson.*

Fig. 114. Collared peccary, *Tayassu tajacu. Photo by N. Woodman.*



is likely they were from collared peccaries. Our group sighted collared peccaries at 200 m and again at 300 m.

At La Selva in August 1988, we observed damage to stems of the large terrestrial aroid, *Dieffenbachia* sp. (Araceae), caused by peccaries feeding on it. As the sap of diffenbachias, and especially this species, contains large amounts of raphides of water-insoluble calcium oxalate crystals and cyanogenic glycosides, this observation is of interest. Because of the high concentrations of these extremely noxious chemicals found in the sap, few insects or vertebrates are able to feed on *Dieffenbachia*. The peccaries seemed to have fed only on the older diffenbachias in which the main stem trailed along the ground. Damage caused by peccaries was noted only on the lowest, horizontal sections of the stem; there was no evidence of feeding on vertical stems. In the northern, arid parts of their range, *T. tajacu* is known to feed on several species of prickly-pear cactus (genus *Opuntia*), which also contain oxalic acid, a substance that is toxic to most mammals (Sowls 1983). Thus, peccaries seem to be one of the few animals that are capable of utilizing plants with high oxalate concentrations.

Family Cervidae

Mazama americana
Red Brocket, Cabro de Monte

Red brocket deer are found from eastern Mexico through Central and tropical South America to Bolivia and Paraguay. In Costa Rica, the subspecies *Mazama americana cerasina* is found throughout the country, although there are few actual records. It frequents forested areas from sea level to near timber line.

We saw tracks of brocket deer at 2,100 m and skulls of this species were seen at a cabin at 2,000 m; presumably these individuals were shot nearby. Brocket deer have been recorded at La Selva on 12 occasions. Tracks of brocket deer in the Zona Protectora were reported by Pringle et al. (1984).

Odocoileus virginianus
White-tailed Deer, Venado Cola Blanca

Two subspecies of white-tailed deer are found in Costa Rica: *Odocoileus virginianus chiriquensis* in the southwest and *O. v. truei* throughout the rest of the country (Fig. 115). White-tailed deer are found from sea level to at least 1,300 m.

There are 21 observations of white-tailed deer at La Selva where they have been recorded from nearly every month of the year. A female with a fawn was observed in January 1984 and a female and two half-grown young were sighted in September 1985. Janzen (1983e) reviewed natural history information for Costa Rica.

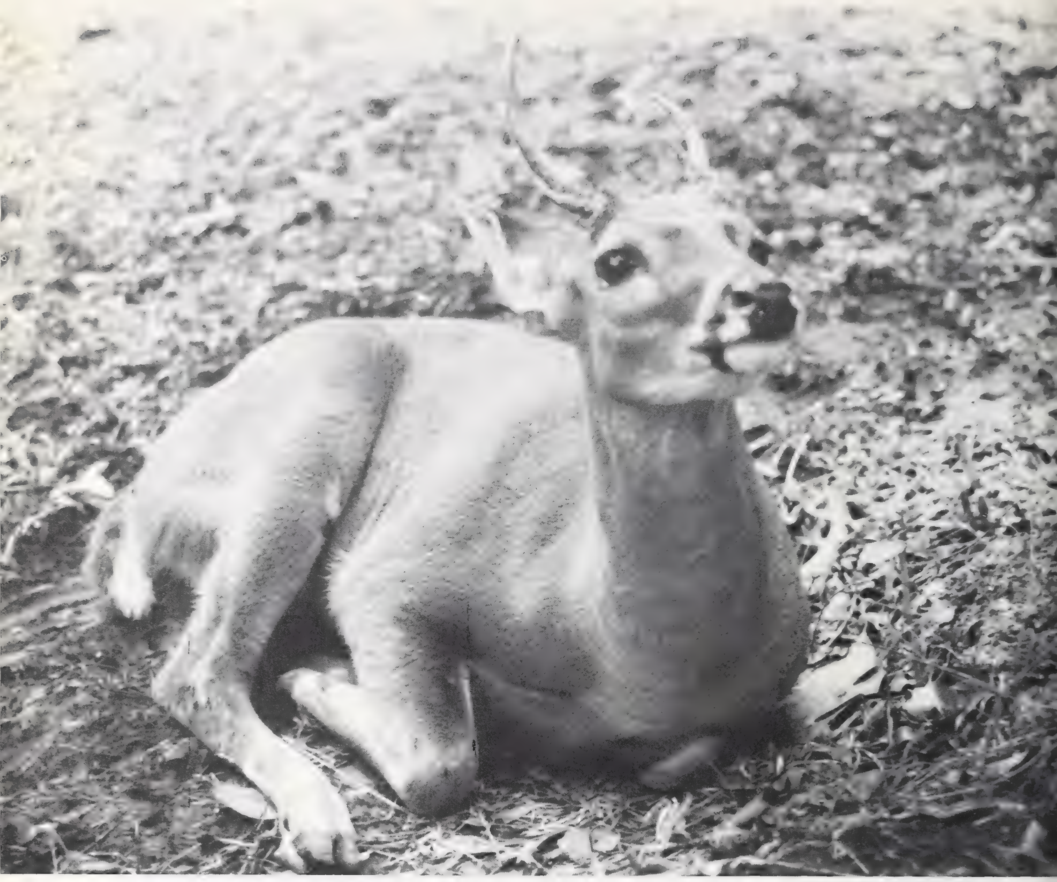


Fig. 115. White-tailed deer, *Odocoileus virginianus. Photo by B. L. Clauson.*

Species Extirpated from the Park

Myrmecophaga tridactyla
Giant Anteater, Oso Caballo

Giant anteaters originally were found from Guatemala and Belize throughout the tropical lowlands of Central America and tropical South America to southwestern Brazil (Fig. 116). The subspecies *Myrmecophaga tridactyla centralis* was found in Central America, but its range is now much reduced due to overhunting and habitat destruction. There are few records or observations of giant anteaters from this region, and we suspect that this species is either extirpated from this area as it is from much of the country, or that population numbers are so low that the population cannot be considered viable.

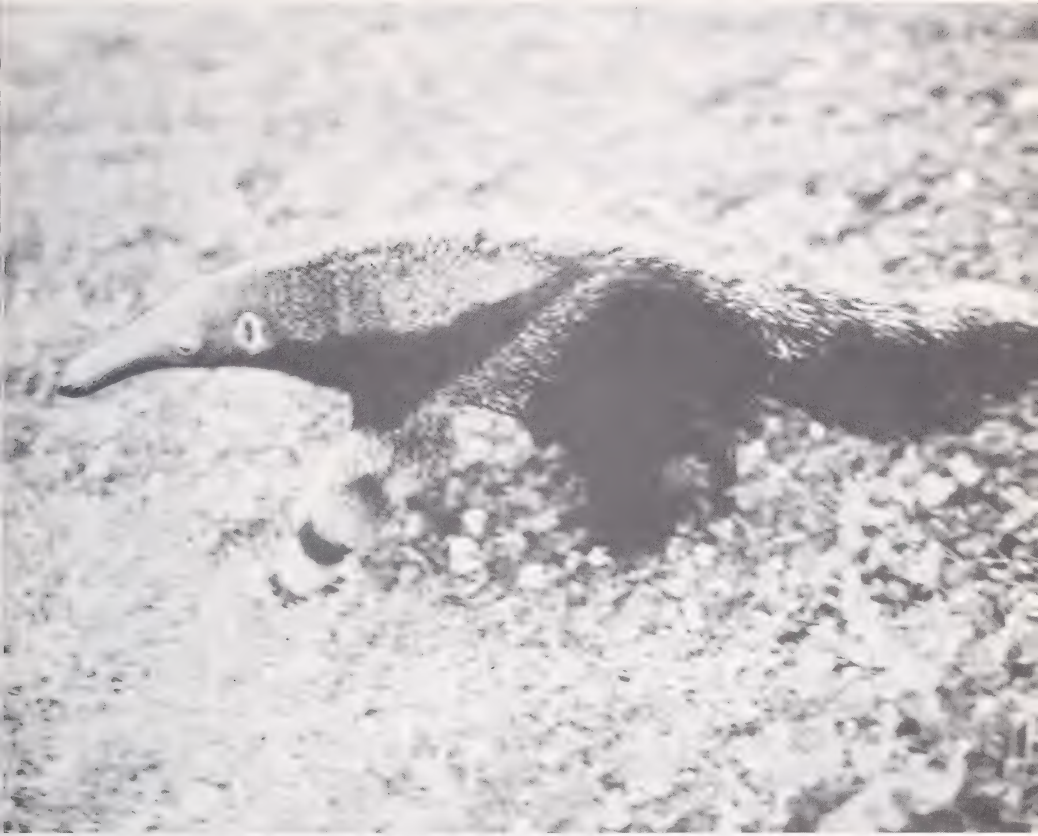


Fig. 116. Giant anteater, *Myrmecophaga tridactyla. Photo by B. L. Clauson.*

In late 1978 or early 1979 McDade observed a large, dark animal at La Selva that she believed was a giant anteater. She noted that it was at least 75 cm high at the shoulders, had a very long and coarsely bushy tail, and had a flash of white near the front legs. It was seen on the River Road Trail between the Quebrada El Sura bridge and the old field station. She saw it on the trail and as it loped into the forest (McDade, personal communication). The only other recent observation of a giant anteater in Costa Rica was one seen near the Sirena field station at Parque Nacional Corcovado on the Osa Peninsula. Boinski saw one at close range while it foraged in maturing second growth forest in 1979 (Boinski, personal communication). On two or three other occasions she observed diggings in termite mounds that she attributed to *M. tridactyla*.

We know little about the original distribution and abundance of giant anteaters in Costa Rica. The first, and one of the few, authors to mention giant anteaters in the country was Alston (1879–82) who reported that they were considered rare in Costa Rica and confined to the "low hot forest lands near the coast." This species has experienced severe reduction in numbers and range since colonization of the Neotropics by European man.

Species of Possible or Probable Occurrence in the Area

Diclidurus albus
Ghost Bat

Ghost bats are found from Nayarit, Mexico, to eastern Brazil. The subspecies *Diclidurus albus virgo* is found in Costa Rica. Although some authors consider *D. virgo* (type locality, Escazú, Costa Rica) a species distinct from *D. albus*, we follow Honacki et al. (1982) in regarding the Central American populations as a subspecies of the widely distributed *D. albus*.

Relatively little published information is available on the natural history of ghost bats. Most of the few specimens of *D. albus* in collections have been shot in flight or from roosting sites under palm leaves (Sánchez and Chávez 1984). In Venezuela, Handley (1976) found them in a variety of habitats. This species is insectivorous. The reproductive cycle seems to be monestrous, and breeding aggregations suggesting harems have been reported (Sánchez and Chávez 1984). Although there are no specimens of ghost bats from the La Selva area, we suspect that it occurs there.

Underwood collected the first Costa Rican specimen at Escazú in 1897 (Goodwin 1946). The biology of ghost bats was reviewed by Ceballos and Medellín (1988).

Aotus lemurinus
Night Monkey, Mono Nocturno

Night monkeys of the genus *Aotus* are widespread in the lowlands of South America and previously were known as far north as Isla Bastimentos, Bocas del Toro Province, Panama. A historical record of an *Aotus* collected in Costa Rica in the early 1870's has long been discounted, as has one from Bluefields, Nicaragua. However, in a recent review of this literature, Timm (1989) suggested that the Costa Rican specimen might be a valid record. Previous authors have attributed this specimen to a locality variously spelled Quindín, Quindin, or Quindiu. This locality (actually in Colombia) was erroneously applied to the specimen by Elliott some 45 years after the specimen was collected. Several recent observations between 1975 and 1986 suggest that *A. lemurinus* may be present in the Caribbean lowlands of Costa Rica (Timm 1989). Night monkeys apparently have been sighted on three occasions at the La Selva Biological Reserve, and hunters have reported night monkeys near that area and also near Bribri, Limón Province, near the Panamanian border. Although the presence of night monkeys in Costa Rica still needs to be confirmed, the species should be sought in appropriate habitats throughout the Caribbean lowlands.

Sciurus deppei
Deppe's Squirrel, Ardilla de Miravalles or Chiza Negra

Deppe's squirrel is found from Tamaulipas and Veracruz of eastern Mexico to northern Costa Rica. A single subspecies, *Sciurus deppei miravallensis*, has been described from Costa Rica; the type locality is Volcán de Miravalles in the Cordillera de Guanacaste at 1,500 ft (Harris 1931, 1943). The distribution of this squirrel in Costa Rica is poorly understood. We have observed it throughout much of the Guanacaste lowlands of northwestern Costa Rica and at Monteverde, where it is quite abundant.

Although the only published records of this squirrel are from extreme northwestern Costa Rica (McPherson 1985), squirrels identified as *S. deppei* have been recorded at La Selva on several occasions. We cannot confirm that *S. deppei* occurs as far east and south in Costa Rica as La Selva; however, we suspect that this species is more widely distributed in the country than believed previously.

Oryzomys couesi
Coues' Marsh Rice Rat, Ratón

Coues' marsh rice rat is found from southern Texas and eastern Mexico to the Caribbean lowlands of extreme northern Colombia (Hershkovitz 1987). The systematic position of *Oryzomys couesi* has long been in a state of flux. It was originally proposed as a full species based on specimens taken in Guatemala; however, Hall (1960) suggested that the populations known as *couesi* from Central America intergraded with *O. palustris* to the north and were best considered a subspecies of *O. palustris*. Recent karyologic studies have demonstrated that *O. couesi* has a large submetacentric X chromosome, whereas *O. palustris* has a large acrocentric X; both have a diploid number of 56 (Benson and Gehlbach 1979). Both karyotypes are known from Texas and Mexico which suggests that two species are involved, although they have not been obtained from the same locality.

Although no specimens of this species have been observed at La Selva or in Braulio Carrillo, it seems likely that *O. couesi* does occur there because it is widely distributed throughout the Caribbean lowlands of Central America and has been collected at several localities in the Caribbean lowlands of Costa Rica. Rice rats are often abundant in cultivated fields and in weedy gardens.

Urocyon cinereoargenteus
Gray Fox, Tigrillo or Zorra Gris

Gray foxes are among the most widely distributed of the New World carnivores, being found from southern Canada across most of the United States (except for the northwestern States) through Mexico and Central America to northern Colombia and Venezuela. Little has been published on the distribution or ecology of gray foxes in the tropics. They may be found throughout the middle and higher elevations of Costa Rica. They appear to be most common in altered habitats. Although we have no records of gray foxes from Parque Nacional Braulio Carrillo, we suspect that they occur there. Apparently these foxes are found throughout the country except for the Atlantic lowlands. The biology of gray foxes, based primarily on studies in the eastern United States, recently was reviewed by Fritzell and Haroldson (1982).

Acknowledgments

We are pleased to thank the Servicio de Parques Nacionales, especially F. Cortés and the many park guards, for making our studies in Parque Nacional Braulio Carrillo possible, profitable, and enjoyable. E. López Pizarro and G. Canessa Mora of the Departamento Vida Silvestre facilitated permits for our work. The Organization for Tropical Studies, especially R. Butterfield, G. S. Hartshorn, L. A. McDade, and C. E. Schnell went above and beyond the call of duty to provide first-rate and indispensable logistic assistance. Funding for this project was provided by the Field Museum of Natural History, National Geographic Society, Organization for Tropical Studies, Rice Foundation of Chicago (we especially thank Mr. and Mrs. A. A. Nolan, Jr.), and Universidad Nacional de Costa Rica. We are extremely grateful to each of these organizations for making our studies possible. We heartily thank R. Aguilar F., J. S. Ashe, R. J. Izor, D. G. Pranke, and J. H. Shook, Jr., for providing excellent technical and logistic assistance in the field, often under trying conditions. R. L. Wenzel provided us with the identifications of the bat flies we collected, and J. E. Keirans provided us with the identifications of the ticks. S. Boinski, A. P. Brooke, G. Hartshorn, D. H. Janzen, and L. McDade freely shared their unpublished observations on mammals with us. J. Rodriguez (University of Costa Rica), S. B. George (Natural History Museum of Los Angeles County), J. S. Findley and T. L. Yates (University of New Mexico), J. K. Jones, Jr. and R. D. Owen (Texas Tech University), P. Myers (University of Michigan), B. D. Patterson (Field Museum of Natural History), D. A. Schlitter (Carnegie Museum of Natural History), and B. Stein and J. L. Patton (Museum of Vertebrate Zoology) were extremely helpful in making specimens housed in their respective collections available to us for study. J. K. Adams, A. L. Gardner, J. Hoth, R. W. McDiarmid, C. Thorington, M. D. Tuttle, and N. Woodman provided us with some of the photographs that are published here. We especially thank J. Wiglesworth for her efforts in expeditiously and cheerfully typing the numerous drafts of this manuscript. M. A. Bogan, G. K. Creighton, A. L. Gardner, G. S. Hartshorn, J. K. Jones, Jr., L. A. McDade, P. A. Opler, D. E. Stone, and N. Woodman provided us with valuable suggestions on earlier drafts. We appreciate the care and expertise A. M. Musser used in drafting the map (Fig. 1).

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61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936–38, by Victor B. Scheffer, 1959. 406 pp.
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